Diversity of morphological and feeding traits in the larvae of Madagascan mantellid frogs

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Chapter 1

General introduction, Results and Discussion

General introduction

1. The tadpole

When discussing amphibian diversity, the majority of studies focus on the adult stage. This is caused by the fact that the larval stage – tadpole – of frogs is not as obvious and attractive as the adults (McDiarmid & Altig 1999). In addition, their study requires sophisticated materials and different methods – as they occupy entirely different niches compared to the metamorphosed frogs –, and is very time consuming. However, these ephemeral and nonreproductive larvae represent the half of the life cycle of amphibians and they live typically in specific aquatic habitats for longer periods than their adults (Altig 1970).

The tadpole, the derived larval stage of anuran amphibians, is one of the most important evolutionary innovations of anurans (Grosjean et al. 2003). The morphological diversity of tadpoles is immense, especially if it is considered that this life history stage is rather simple in overall construction. Larval specialisations include usually keratinized teeth and jaw sheaths, a long coiled intestine, and caudal locomotion. Many of the morphological variations of buccopharyngeal (buccal filters) (Harris 1999) and oral (papillae, labial teeth) features are correlated with the mode of feeding (*e.g.*, carnivorous, suspension feeding, scraping; Orton 1953; Wassersug & Heyer 1988, Altig & Johnston 1989), and with the microhabitat. Understanding the diversity of tadpole morphology is a requisite for successful species identifications.

Most tadpoles are filter-feeding omnivores. Their digestive system is adapted to process vegetable matter (Altig & McDiarmid 1999a). They are able to feed both on the phytoplanktonic community by means of filtration, and on a large variety of substrates (including algae, macrophytes and carrion) by rasping, scraping and chopping with their jaw sheaths and labial teeth (Seale & Wassersug 1979; Seale 1982). Some researchers used morphological features to predict the feeding pattern of the tadpoles. For example, carnivorous tadpoles have reduced branchial filters, buccal papillae, and labial teeth, whereas suspension feeders have the most elaborate buccopharyngeal structures, and suctorial and surface feeding forms have major morphological features associated with feeding, such as a high number of papillae or funnel-shaped mouthparts (Orton 1953; Altig & Johnston 1989). Gut contents are examined to study what tadpoles truly have ingested. Although this does not indicate necessarily what they actually digest, at least parts of their diet and their feeding behaviour might be identified.

The tadpole stage specifically maximizes growth, and tadpoles inevitably metamorphose into juvenile frogs (Wassersug 1974; Slade & Wassersug 1975; Wilbur 1980). Therefore they cannot form stable long-term ecological associations (Alford 1999). Some tad-

Figure 1. Map of Madagascar showing the major collecting sites (Google earth)

poles exploit just relatively simple, predictable habitats such as temporary ponds for having a rapid growth rate while others develop slowly in more complex permanent aquatic habitats. Also, many physical and biological factors influence the spatial and temporal distribution of tadpoles among different microhabitats. They may select their microhabitat because of the attraction to or avoidance of conspecifics and predators (Hoff et al. 1999), but their presence in one area may also be affected by the availability of food. The habitat of tadpole can be predicted by their morphology (*e.g.*, suctorial tadpoles live in faster running waters), but a detailed ecological analysis is needed to understand the most important factors influencing their distribution. Such information is also essential for the elaboration of tadpole eco-morphological guilds.

It is invaluable to analyze how those morphologies are distributed across taxa and which tadpoles have been described in each group. Because of many gaps in our knowledge and the general conservativeness of tadpoles, some tadpoles are more difficult to characterize, and therefore to identify, than others (Altig & McDiarmid 1999b). The examination of the small, complex oral apparatus of a tadpole provides the major characteristics for species identification, however, this is in general very meticulous work. The oral disk is a structure composed of upper and lower labia, usually with transverse tooth ridges surmounted by rows of labial teeth. Marginal papillae occur in various configurations at the edges and submarginal papillae occur in various patterns on the oral disk (Altig 1970). The oral disk and its presumed derivatives are reduced in various ways in tadpoles in several different lineages, and their morphology depends on feeding modes (Altig & McDiarmid 1999a). Some tadpoles have few to no labial teeth but have normal or unusual jaw sheaths. Tadpoles of species with many tooth rows have larger oral disk than those with fewer rows (Altig & McDiarmid 1999a). Often, interspecific variation seems to be only little or is even absent; whether such variation is simply not recognized or poorly understood, and remains to be shown (Altig & McDiarmid 1999b). For example, conspecific tadpoles collected from turbid versus clear water vary tremendously in color, and captive bred tadpoles often have aberrant mouthparts compared to wild-caught individuals of the same species. The captive breeding of tadpoles or using them in experimental situations in the laboratory is often rather easy, but doing these things in the field to produce typical specimens as they are found in the wild is difficult (McDiarmid & Altig 1999).

Great efforts in classifying tadpoles via different criteria have been made by different authors. For example, Orton (1953) considered that tadpole types were derived from a generalized form (a typical lentic-benthic tadpole) and defined four major types based on patterns of mouthpart and spiracular morphology. Other ecomorphological guilds were based on ecological, geographical, and taxonomical data (*e.g.*, Van Dijk 1972; Lamotte & Lescure 1989).

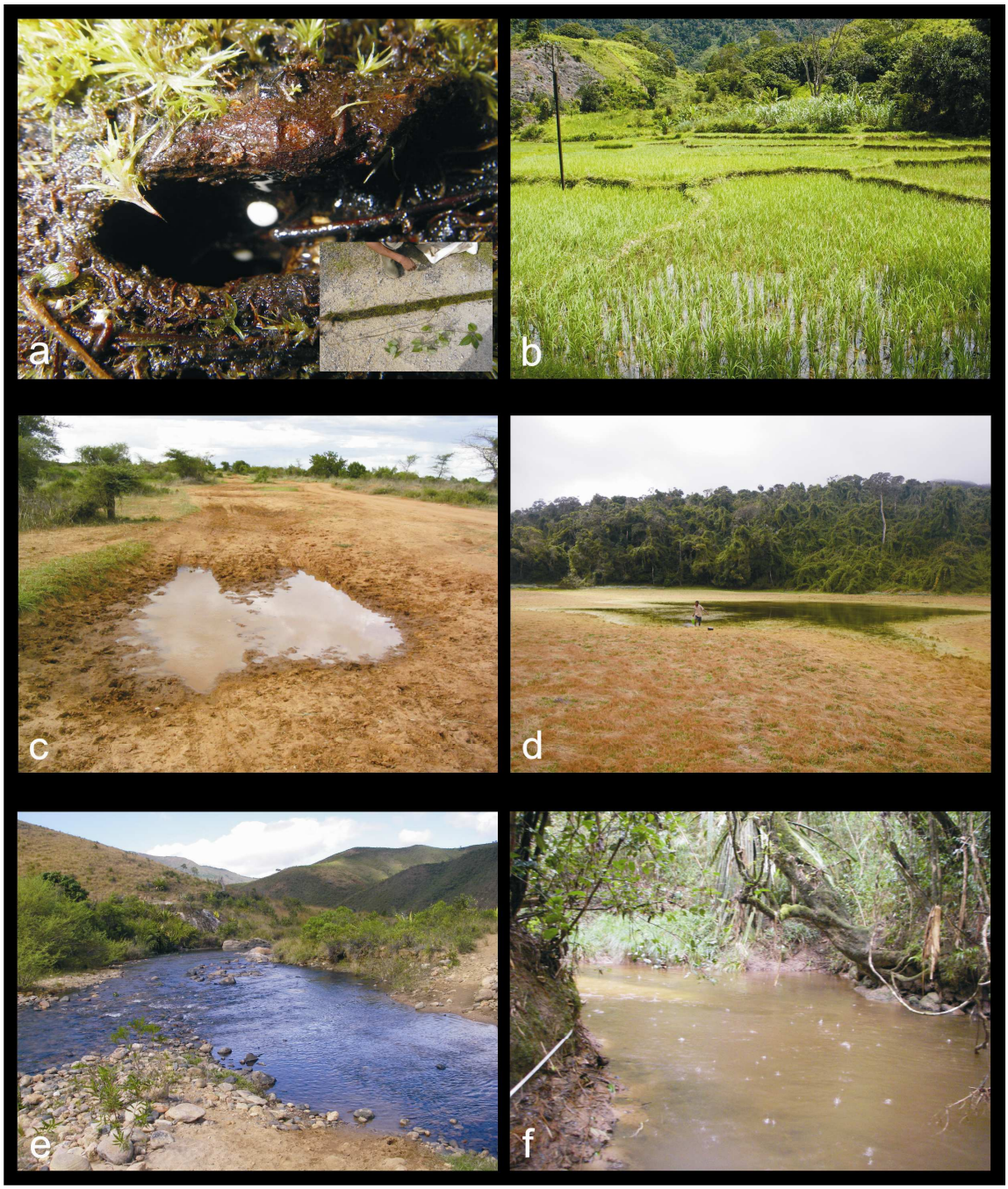

Figure 2. Different habitat of frog larvae: **a** – Tree hole in Ranomafana, habitat of microhylid larvae; **b** – Ricefield in Ranomafana, habitat of the tadpoles of *Ptychadena mascarienensis*; **c** – Temporary stagnant water in the dry spiny forest in the south of Madagascar, habitat of the tadpoles of *Laliostoma labrosum*; **d** – Temporary stagnant water in the highest mountain Tsaratanana, habitat of the tadpoles of *Heterixalus*; **e** – River outside the forest in Ankijagna Lalagna, habitat of the tadpoles of *Boophis sambirano* [Ca49] and *Boophis sambirano* [Ca50]; **f** – Stream in Ranomafana National Park, habitat of many lotic tadpoles.

Altig & Johnston (1989) considered the source of energy as the ultimate discriminator of anuran developmental modes and they used some additional parameters – such as tadpole morphotypes, activities of hatchlings, and young larvae, etc. – to extend their classification. Accordingly these authors established six endotrophic (in which the developmental process is accomplished completely by the maternal source of energy) and 15 exotrophic (in which the developmental process is accomplished via ingested food). Although this is a much elaborated classification, these different guilds are still not enough to classify many newly identified tadpoles due to their new characters or patterns which were not known at the time when these classifications were defined.

The larval stages are unknown in many species of frogs and the number of anuran species is still increasing in tropical regions. Attributing newly captured tadpoles to a probable species or even attributing hatched tadpoles from a clutch that was found close to an adult frog to the respective species likely leads into a false species assignment. The best way to overcome this impediment is using DNA barcoding for species identification. In some cases the larval stage is the basis for a taxonomic classification (with the adult stage being unknown at the time of the study), which is defined as 'reverse taxonomy' (Markmann & Tautz 2005).

2. The case of Madagascar

The amphibian fauna of Madagascar is highly exceptional and characterized by its high endemicity, with 100% of the native species being endemic to the island (Glaw & Vences 2007). Madagascan amphibians are composed by five families of frogs: Dicroglossidae, Ptychadenidae, Hyperoliidae, Microhylidae, and Mantellidae.

Based on molecular studies, the last four families are considered to be endemic to the island, whereas the family Dicroglossidae comprising just one species *Hoplobatrachus tigerinus* is introduced (Glaw & Vences 2007). The single species *Ptychadena mascareniensis*, a member of the family Ptychadenidae has been assumed to be introduced from the African mainland. However, recent molecular studies revealed that *P. mascareniensis* populations from Madagascar represent a clade being different from the African ones and presumably constitute another species (Vences et al. 2003, 2004). The family Hyperoliidae is present on Madagascar only with the genus *Heterixalus* which comprises eleven species inhabiting grassland, rice fields, and forest edges (Glaw & Vences 2007).

The family Microhylidae is represented by the three subfamilies Cophylinae (*Anodontohyla, Cophyla, Madecassophryne, Platypelis, Plethodontohyla, Stumpffia*, and *Rhombophryne*), Dyscophinae (*Dyscophus*), and Scaphiophryninae (*Paradoxophyla* and *Scaphiophryne*). Cophylines are closely tied to rainforest habitats and have a reproduction characterized by parental care. Within this group, a huge variety of life history traits exists: arboreal (*Anodontohyla*, *Cophyla*, *Platypelis*, and

Figure 3. Working team: **a** – Ecological survey in Isalo National Park; **b** – Ecological survey in Ranomafana National Park; **c** – E. Reeve taking picture of the tadpole buccal anatomy; **d** – R.D. Randrianiaina taking picture of the oral disk; **e** – R.D. Randrianiaina drawing the tadpole of *Mantidactylus femoralis*; **d** – Samples of tadpole drawing hanging on wall.

Plethodontohyla), terrestrial-fossorial (*Madecassophryne* and *Rhombophryne*), and miniaturized terrestrial forms (*Stumpffia*) (Glaw & Vences 2007). The non-cophyline species differ from cophylines in their habitat preferences as they are mainly terrestrial, although some species are partly rupicolous. They live mainly in open areas and some species occur in the arid and sub-arid area of western and south-western Madagascar (Glaw & Vences 2007).

The Mantellidae form the largest family of Malagasy frogs both in terms of species richness and diversity in morphology, ecology, and reproductive modes. Mantellids are endemic to Madagascar and the Comoro island of Mayotte where two undescribed endemic species occur. This family comprises three major and well defined lineages (Figure 9) corresponding to the three subfamilies Boophinae (*Boophis*), Laliostominae (*Aglyptodactylus* and *Laliostoma*), and Mantellinae (*Blommersia, Wakea, Mantella, Guibemantis, Spinomantis, Gephyromantis, Tsingymantis*, *Boehmantis*, and *Mantidactylus*) (Glaw & Vences 2007). Molecular data have provided strong evidence that all taxa included in the Mantellidae form a monophyletic group, and that their sister group is the Asian family Rhacophoridae.

Within this family, the subfamily Boophinae comprises a single genus, *Boophis*, including 72 nominal species and 25 candidate species distributed in 10 main species groups: *Boophis tephraeomystax* group, *Boophis microtympanum* group, *Boophis majori* group, *Boophis goudoti* group, *Boophis albilabris* group, *Boophis luteus* group, *Boophis albipunctatus* group, *Boophis rappiodes* group, *Boophis mandraka* group, and *Boophis ulftunni* group (Glaw & Vences 2007; Wollenberg et al. 2008). They are typically known as treefrogs which breed in running water, with the exception of the *Boophis tephraeomystax* group. Whereas the highest diversity of this genus is found in the eastern rainforest, they also include species which are specialized to xeric conditions in western Madagascar (two species of the *Boophis tephraeomystax* group: *Boophis doulioti* and *Boophis xerophylus*) and to high-altitude ericoid vegetations above the tree line (three species of the *Boophis microtympanum* group: *B. microtympanum*, *B. laurenti*, and *B. williamsi*).

The two genera of the subfamily Laliostominae, *Aglyptodactylus* (three species) and the monotypic *Laliostoma* are mainly terrestrial and breed in temporary ponds, often explosively in large aggregations. While *Laliostoma* is a typical species of the arid western and southern habitats, *Aglyptodactylus* is common in eastern rainforests as well as in western deciduous forests.

The species of the subfamily Mantellinae are characterized by a derived reproductive behaviour in which no amplexus occurs and the male positions itself above the female. This mating behaviour is very likely associated to the presence of structures commonly called 'femoral glands' on the ventral side of their shanks (Vences et al. 2007). This family contains more than 120 nominal species and also more than 120 candidate species distributed in nine subgenera: *Blommersia, Wakea, Mantella, Guibemantis, Spinomantis, Gephyromantis, Tsingymantis*, *Boehmantis*,

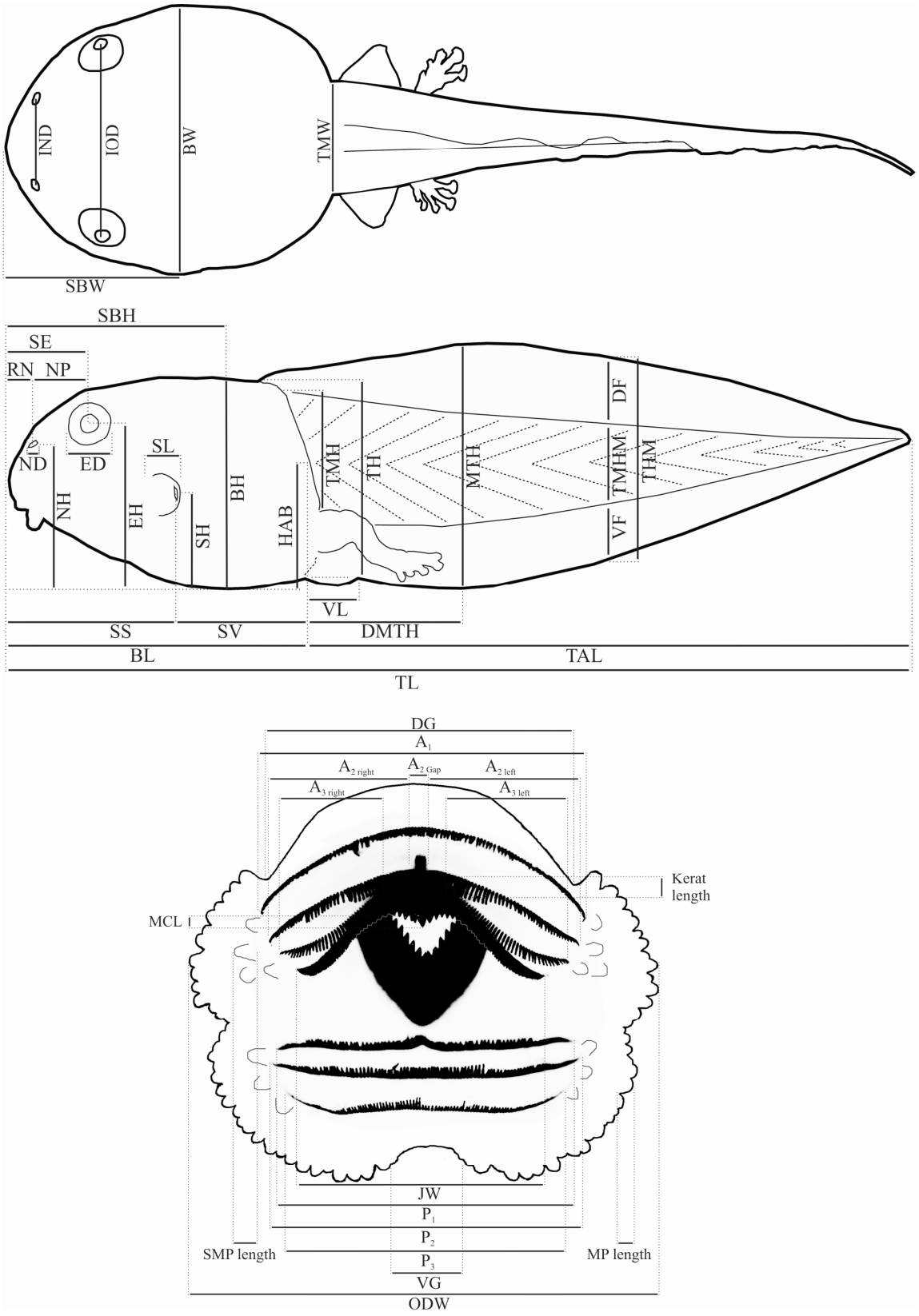

Figure 4. Drawings representing the landmarks of the measurement: **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

and *Mantidactylus*. The subgenera *Wakea, Tsingymantis,* and *Boehmantis* are monospecific. Although the reproduction of *Wakea* and *Boehmantis* is unknown, *Tsingimantis* larvae were found developed in karstic limestone. *Blommersia* and *Guibemantis* are mainly arboreal frogs and have generalized tadpoles living in open water. Exceptions are some species whose larvae develop in confined nests, such as *Pandanus* leaf axes. *Mantella* species have extrophic tadpoles with the exception of *Mantella laevigata* larvae which develop in bamboo holes. Also *Spinomantis* consists of species with exotrophic tadpoles and includes Madagascan biggest tadpole (*Spinomantis elegans*). *Gephyromantis* is divided into five subgenera (*Gephyromantis*, *Vatomantis*, *Laurentomantis*, *Phylacomantis*, and *Duboimantis*) and contains a number of frog species that to a varying degree evolved independence from waterbodies for reproduction. Some species (in the subgenera *Phylacomantis* and *Duboimantis*) have free swimming, exotrophic tadpoles in streams, whereas other tadpoles (subgenus *Gephyromantis*) are nidicolous. There is also presumed direct-developing species. The genus *Mantidactylus* is subdivided into six genera: *Mantidactylus*, *Brygoomantis*, *Ochthomantis*, *Maitsomantis*, *Chonomantis* and *Hylobatrachus*. All of these groups have tadpoles living in the streams, but in most groups (except *Brygoomantis*) these tadpoles have specialized mouthpart morphologies (Glaw & Vences 2007).

Why is it useful to study Madagascan tadpoles? It is useful to study them because *(1)* they are of prime importance for aquatic ecosystems in Madagascan forests due to a virtual absence of fishes in the majority of them. They occur in all kind of water bodies, even outside the forest, in rice fields and sometimes in temporary stagnant waters (Figure 2). *(2)* The high frog diversity might partly originate from the ability of expansion and adaptation of the larval stage in different microhabitats, and *(3)* the morphology of tadpoles reflects their habitat, which is an important factor of the spatial distribution of the adults; *e.g.*, endotrophic tadpoles do not develop in water bodies and therefore the adults do not live necessarily near water bodies. In contrast, adults with exotrophic tadpoles are often observed near water bodies.

Historically, the research on Madagascan amphibians was started in 1838, when Tschudi published the description of an adult frog named *Boophis goudoti*, whereas the study of larval stages began only 130 years later with the works of Razarihelisoa in the 1970's. Since this time, the research activities on tadpoles can be classified into four main eras: *(1)* the **Old era** was characterized by the works of Razarihelisoa (1969, 1974a, b) and Blommers-Schlösser (1975, 1979a, b) with surveys of larval developmental processes and some larval descriptions; *(2)* the **Middle old era** was represented mainly by the work of Blommers-Schlösser & Blanc (1991), and Glaw & Vences (1994) who were more focusing on larval descriptions but conducted only a few surveys; *(3)* the **New era** from 2003 to 2006 was characterized by several descriptive (Raharivololoniaina et al. 2003, 2006; Glos et. al. 2005; Thomas et al. 2005, 2006; Altig &

Figure 5. Diversity of tadpoles in the family Mantellidae (dorsal, lateral and ventral views of live specimens): a – *Gephyromantis tschenki*; **b** – *Boophis periegetes*; **c** – *Spinomantis* sp. 2; **d** – *Boophis schuboeae*; **e** – *Boophis marojezensis*; **f** – *Gephyromantis azzurrae*; **g** – *Mantidactylus femoralis*; **h** – *Mantidactylus mocquardi*; **i** – *Mantidactylus cowanii*; **j** – *Mantidactylus majori*; **k** – *Boophis picturatus*; **l** – *Mantidactylus aerumnalis*. The scale bars represent 1 mm.

McDiarmid 2006; Grosjean et. al. 2006; Mercurio & Andreone 2006; Randrianiaina 2006; Vejarano et al. 2006a, b, c) and ecological (Glos & Linsenmair 2004, 2005) works of young researchers; and *(4)* the **Modern era** since 2007 is being characterized by active and very intensified researches on Madagascan tadpoles (Figure 3).

Despite all the efforts provided during the first three eras, larval stages of many amphibians are still poorly known. Of the 273 described species and the approximately 200 known but still undescribed candidate species (Vieites et al. 2009), until recently tadpoles of only 90 species were described. To resolve this problem, a project aimed to increase the knowledge of the larval stages of the highly diversified frogs of Madagascar by studying the diversity of their morphology, ecology, behavior, feeding traits, and oral anatomy was set up in 2007.

The morphological (Figure 5) and oral anatomy (Figures 6 and 7) studies were based on previously and freshly (from 1996 to 2010) collected specimens from different areas of the country (Figure 1). These areas can be classified into three categories: *(1)* mid elevation areas between 800 to 1000 m a.s.l., such as the Ranomafana region and the Andasibe- An'Ala complex which are characterized by their high degree of microendemism and species richness, due to the fact called Mid-domain effect (Vences et al. 2009); *(2)* high altitude and isolated mountains from 1000 to 2900 m a.s.l., such as the Manongarivo-Tsaratanana complex, Marojejy, Montain d'Ambre, Ankaratra, and Andringitra – presumed to be refugia from climate change – which are characterized by a higher endemism in species adapted to higher elevations (Vences et al. 2009); *(3)* western isolated forests, such as Isalo, Kirindy, and Ambohitantely being affected by the vicariant speciation schemes (Vences et al. 2009); *(4)* offshore islands, like Nosy be and Nosy Mangabe considered as important due to their status as type locality of several amphibian and reptile taxa (Andreone et al. 2003); and *(5)* forest fragments such as Mahasoa and Vevembe. Tadpole ecological surveys were carried out in 2007 and 2008, and behavioral experiments of different tadpole guilds were realized in 2009 in Ranomafana National Park. In addition, tadpoles used for the gut content and isotope analyses were captured there also. This area was chosen as it is characterized by its high degree of endemism and species richness and furnishes adequate facilities for such purposes. Experiments on the behavior of the carnivorous tadpoles of *Gephyromantis azzurrae* were accomplished in Isalo as the species is endemic for this region. All tadpole series selected by our team were subsequently identified by DNA barcoding in the laboratory of the Technical University of Braunschweig, and their identification confirmed by matching the tadpole DNA sequences to the sequences from well-identified adults. This DNA barcoding work, in particular the comparisons of sequences using the BLAST algorithm, was mainly carried out by A. Strauss, and the laboratory work by G. Keunecke, M. Kondermann, and E. Saxinger.

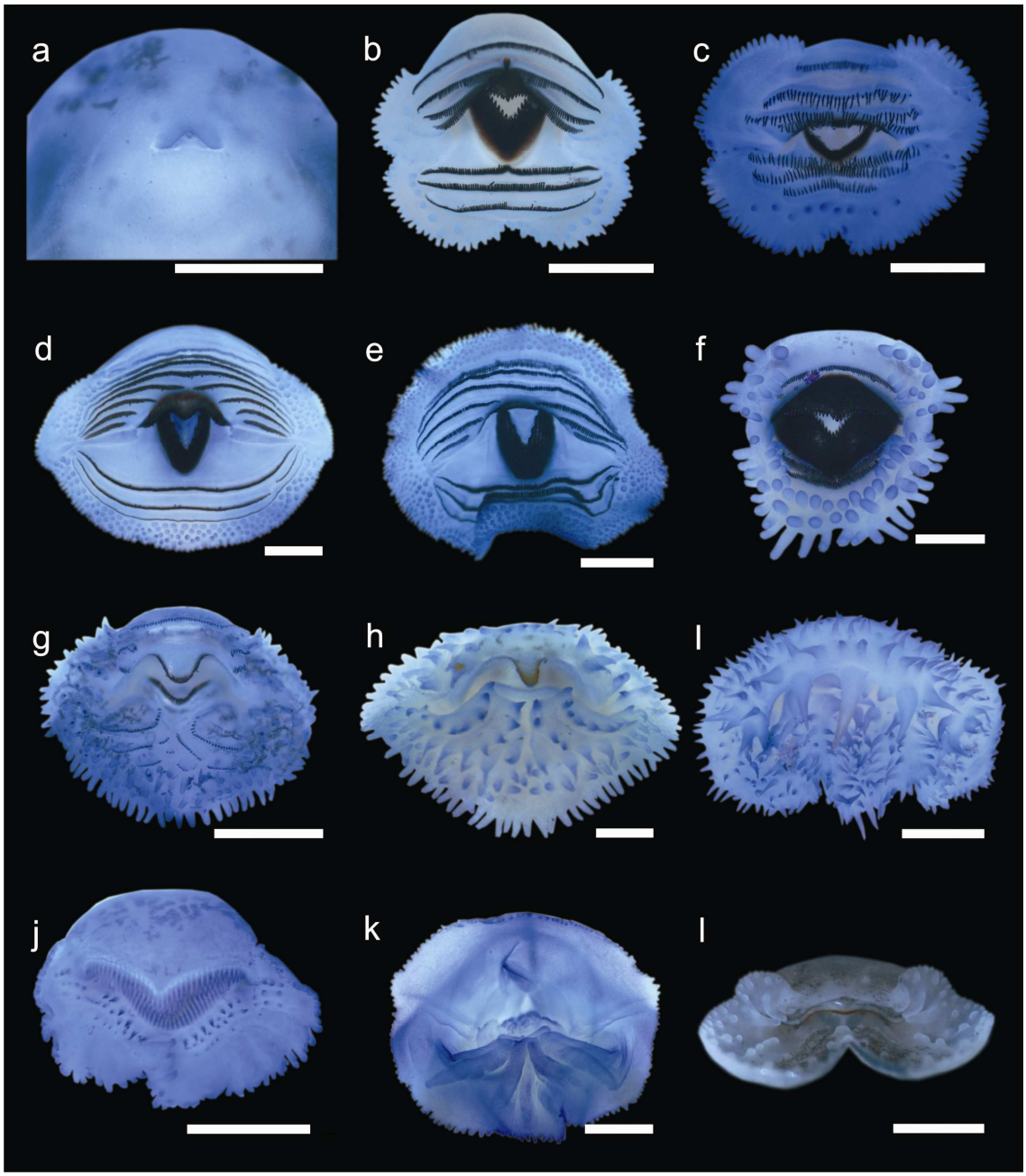

Figure 6. Diversity of oral disk structures in tadpoles of the Mantellidae (stained with methylene blue): **a** – *Gephyromantis tschenki*; **b** – *Boophis periegetes*; **c** – *Spinomantis* sp. aff. *fimbriatus*; **d** – *Boophis schuboeae*; **e** – *Boophis marojezensis*; **f** – *Gephyromantis azzurrae*; **g** – *Mantidactylus femoralis*; **h** – *Mantidactylus mocquardi*; **i** – *Mantidactylus cowanii*; **j** – *Mantidactylus majori*; **k** – *Boophis picturatus*; **l** – *Mantidactylus aerumnalis*. The scale bars represent 1 mm.

Many prominent successes have already been achieved in this Modern era. Many articles concerning tadpole morphological descriptions, behavior, and ecology have already been published: Randrianiaina et al. (2007) led to a new perception of the genus *Gephyromantis* – which was formerly considered as having a direct development mode – by describing the carnivorous tadpole of *G. pseudoasper* and the generalized tadpole of *G. ambohitra*; Glos et al. (2007a, b, 2008) studied the behavior of tadpoles from the dry-forest in the Western Madagascar; Glos et al. (2007c), Schmidt et al. (2008), Randrianiaina et al. (2009a, b), and Rasolonjatovo et al. (2010) contributed further descriptions of *Boophis* tadpoles; Grosjean et al. (2007, 2009) focused on the description of microhylids tadpoles; Jovanovic et al. (2009) described the larval stages of the aposematically colored frogs of the genus *Mantella*; Schmidt et al. (2009a, b) described five tadpoles of the subgenus *Brygoomantis* (*Mantidactylus*) and *Laliostoma labrosum*, respectively, and Andreone et al. (2010) reported the development of the larval stage of a new species of *Blommersia* in a fallen palm tree. The PhD study of A. Strauß concerning the tadpole ecological survey in Ranomafana National Park was supported in 2010. His works provided ecological data on stream dwelling larvae and their communities (Strauß et al. 2010), summarized the species distribution and community structure of anuran larvae in rainforest stream (Strauß et al. in prep.), and emphasized the impact of seasonal changes on functional and phylogenetic diversity of Madagascan tadpole communities (Strauß et al. in prep.). Two important articles have just been published earlier this year. Reeve et al. (2011) revealed the very surprising and fascinating behaviour of the carnivorous tadpoles of *Gephyromantis azzurrae* from Isalo National Park by showing that these tadpoles actively emit clicking sounds during competitive feeding, whereas Grosjean et al. (2011) accentuated the close morphological similarity of the tadpoles of *Mantidaclylus* (subgenus *Chonomantis*).

Results and Discussion

My own work within the framework of this research program aims to assess the correlations between the diversity of morphology, ecology, and feeding traits in these larvae. Basically, my part was mainly the morphology and in this thesis I am now reporting own data and summarizing the results of the morphological study of tadpoles of the family Mantellidae from Madagascar, especially focusing on three groups (rheophilous *Boophis*, *Ochthomantis*, and *Gephyromantis*). The whole work was realized at the Zoological Institute of the Technical University of Braunschweig.

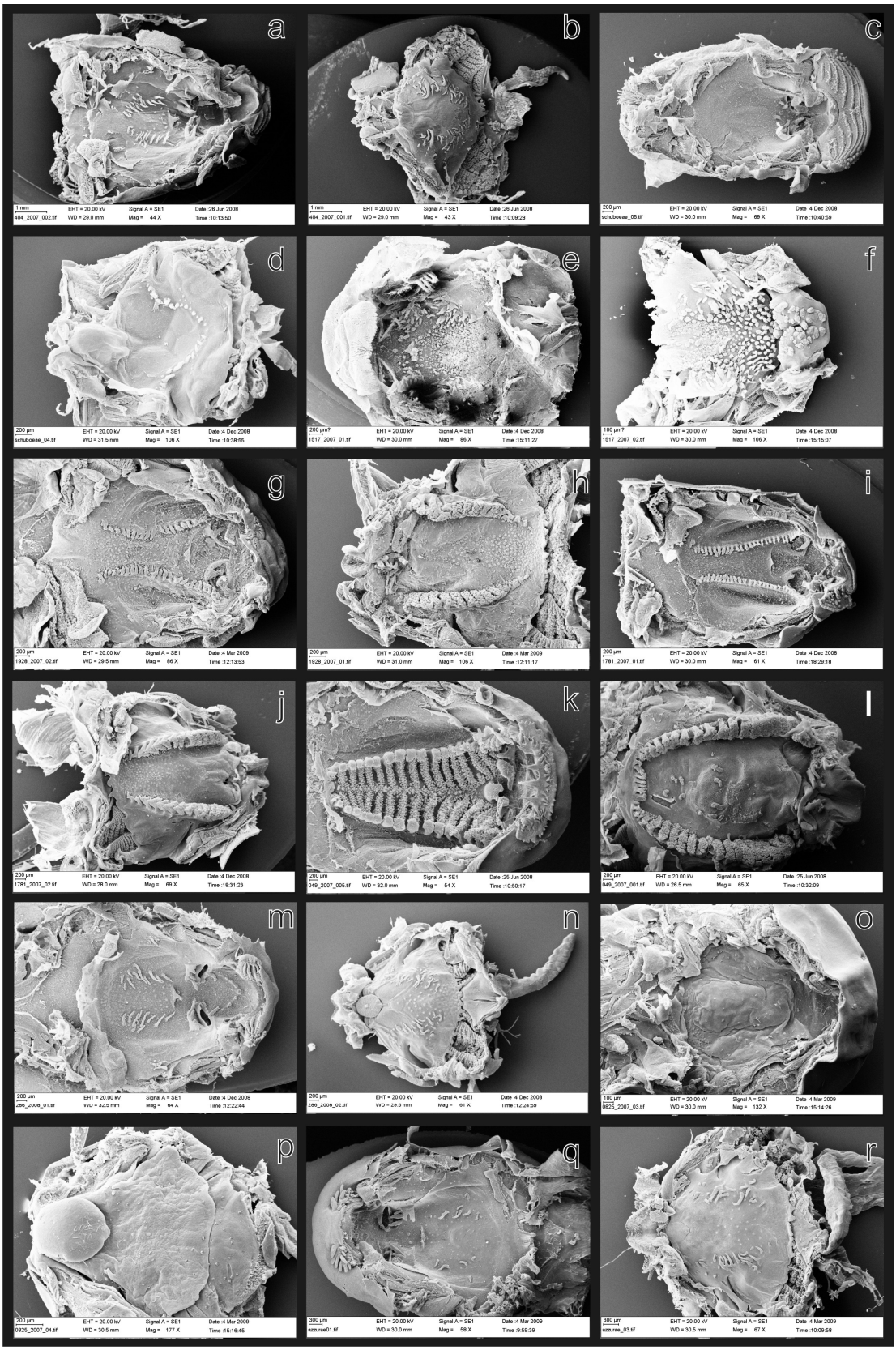

Figure 7. Diversity of buccal anatomy (buccal roof and floor respectively): Scanning electron microscope pictures produced by E. Reeve at the Dresden Zoological Museum: **a-b** – *Boophis periegetes*; **c-d** – *Boophis schuboeae*; **e-f** – *Boophis picturatus*; **g-h** – *Mantidactylus femoralis*; **i-j** – *Mantidactylus mocquardi*; **k-l** – *Mantidactylus majori*;; **m-n** – *Gephyromantis ambohitra*; **o-p** – *Gephyromantis granulatus*; **q-r** – *Gephyromantis azzurrae*

1. Tadpole diversity in Mantellidae

The data gathered in the framework of this thesis confirm that mantellid frogs have free living larvae except *Mantella laevigata*, *Blommersia angolafa* and *Guibemantis* whose tadpoles develop in tree holes and phytotelmata, and some species of *Gephyromantis* which have larvae developing in terrestrial nests. Almost all genera, or species-groups in the case of *Boophis*, have a recognized typical tadpole form, making it relatively easy to distinguish them from tadpoles of other genera or species groups. Due to the morphological similarity of the tadpoles within a genus or species group, a determination at species level is sometimes very difficult or even impossible. Only high standard and detailed descriptions with including various morphological characters (Figure 4, Appendix 3-Table 13) and additional high level meticulous drawings can highlight morphological differences between many species. Sometimes the only difference between two species may lie in pigmentation patterns; *e.g.*, between the different *Boophis sambirano*-like and *Boophis marojezensis*-like tadpoles in **Chapter 2**, and the different *Mantidactylus femoralis*-like and *Mantidactylus mocquardi*-like tadpoles in **Chapter 4**.

2. Food and feeding behaviour

The detailed study of tadpole diet is a new subject of Madagascan amphibians research. As tadpole diet can be predicted by the morphology of the oral disk, this study presents new insights on this subject.

It is hypothesized that a non-feeding tadpole should have a reduced oral disk; *i.e.*, a lack of all usual components of the oral disk or even have an obstruct oral disk. This hypothesis was confirmed in tadpoles of five species of *Gephyromantis*: *G. granulatus*, *G. sculpturatus*, *G. tschenki*, *G. ventrimaculatus*, and *G. blanci* [Ca6 Glaw & Vences 2007] in **Chapter 5**. The fact that the first four tadpoles, which have a small oral disk opening considered as the mouth, were found as free living larvae in a stream has still left some doubt about their non-feeding mode, but rearing individuals of an egg clutch belonging to their sister species to metamorphosis confirmed this hypothesis.

In **Chapter 3**, the outstanding tadpole of *Boophis picturatus* is described, which is characterized by an oral disk lacking all its typical components. The gut content analysis revealed the ingestion of sand particles of this tadpole (Figure 8, page 112). This very unusual feeding mode becomes possible, because the oral structure – just a commodious mouth opening (Figure 5, page 106) – is suitable for sand consumption.

A preliminary result of gut content analysis showed that the tadpoles of *Boophis marojezensis* [Ca51] consume a higher amount of algae in comparison with those belonging to

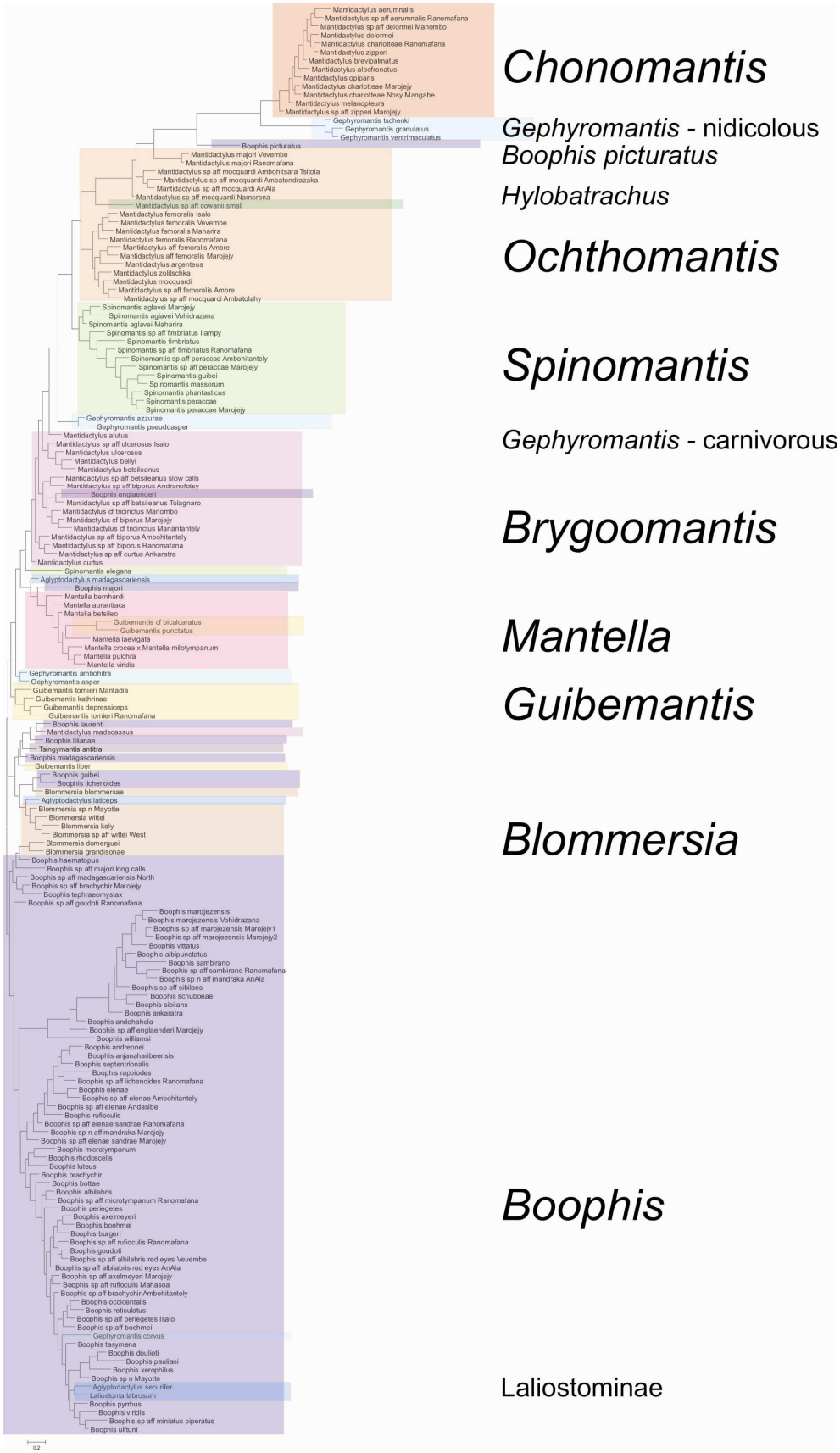

Figure 8. Preliminary phylogenetic tree based on searches under Bayesian inference, using the software MrBayes, based on the full morphological dataset generated in this thesis.

another species, even compared to *Boophis schuboeae* tadpoles which share the same rheophilus pattern (**Chapter 2**). This can be explained by the fact that these suctorial tadpoles maintain continuously their position in the water current via their oral disk that is surrounded by many and complete marginal and submarginal papillae. The longer they maintain their position on the rocky substrate, the more algae they consume as they continuously scrape off the rocks. No evident data about diet and feeding behavior is available for the *Mantidactylus* tadpoles.

The feeding niche of tadpole species was also analyzed by measuring the stable isotope signatures in tadpole tissues (this part of the study is being mainly led by J. Glos from the Biocenter Grindel, University of Hamburg). In detail, the ratios of the stable isotopes carbon and nitrogen were determined *(1)* to indicate the trophic position of a species in the food web (δ15N) and *(2)* to identify major energy sources of this species (δ13C). Our preliminary results indicate major differences between some species (*e.g.*, differences between species of more than one trophic level) but not between others. A more detailed statistical analysis of this data will show up if the feeding niches of tadpoles as determined by stable isotopes correlate either to morphological characters (*i.e.*, of the oral disk) or ecological preferences (*i.e.*, microhabitat choice), or both.

3. Microhabitat preferences

The external morphology predicts the microhabitat preference of tadpoles. Accordingly, tadpoles with high fins, often associated with short tails, live generally in stagnant waters; *e.g.*, the case of *Boophis tephraeomystax* group and *Guibemantis* tadpoles. On the other hand, tadpoles with low fins and a strong caudal musculature live in flowing water with sometimes strong water currents. Rheophilus tadpoles (**Chapter 2**) are adapted to live in rapids due to their ability to attach themselves with their oral disk to the substrate in the water. Even if our ecological analysis did not statistically confirm a true preference for this microhabitat, we could show that in contrast to all other types of tadpoles, species with enlarged oral disks are able to exploit stream sections with strong current.

A very low fin is also favorable for nidicolous tadpoles, as there is a limited space in the nest. The presence of the low fin *Gephyromantis* tadpoles in a lotic microhabitat raises the question if they may need to spend a part of their life cycle in open water.

A kind of camouflage is found in *Boophis picturatus* tadpoles (**Chapter 3**). Their coloration in life of yellowish brown or beige (Figure 3, page 102) is in harmony with their preferable microhabitat sandy substrate, in which most of the specimens have been found.

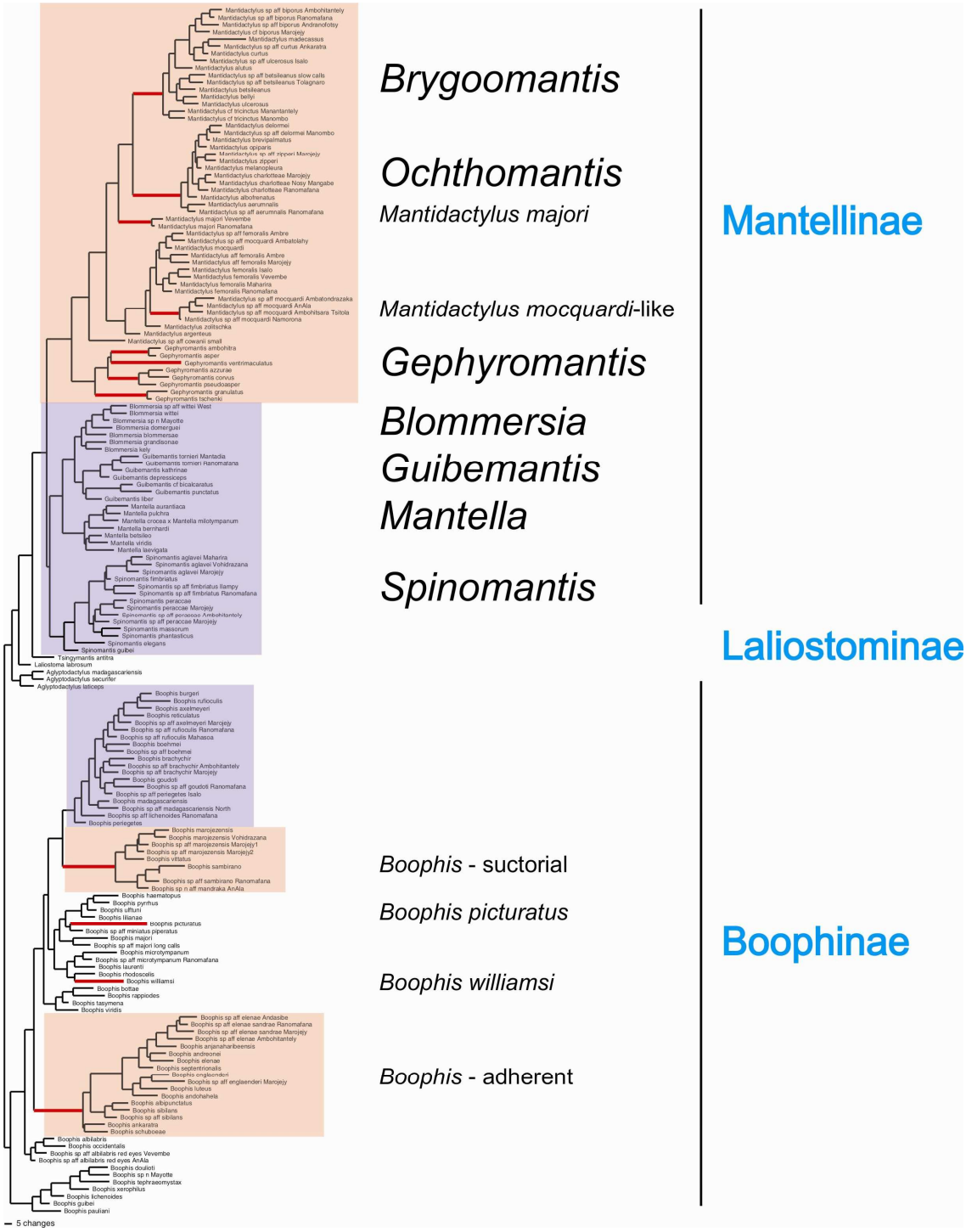

Figure 9. Tree topology based on molecular data. Branch lengths are proportional to reconstructed change in tadpole morphological characters.

4. Morphological and ecological plasticity

Matellid frogs have different types of tadpoles ranging from the generalized to the most derived form: the enlarged oral disk type in Boophinae and the various types with reduced oral disks in Mantellinae. In general a genus, or a species group consists of relatively similar tadpoles, but a high morphological divergence has been found in two groups: the *Boophis majori* group and the genus *Gephyromantis*. The *Boophis majori* group is characterized by having the two extremely derived (the most enlarged and the most reduced) oral disks at the same time, plus the generalized and the reduced form in B. *majori* [Ca35 Glaw & Vences 2007] (see Ecomorphological part). The enlargement of the oral disk in the strongly rheophilus *Boophis* tadpoles is accompanied by the development of the caudal muscle, which is very useful for their general microhabitat. This case shows a tight morphological-ecological plasticity. Almost the same scheme is also found in *Gephyromantis*. This genus is characterized by having three forms of tadpoles; the generalized, the carnivorous, and the non-feeding. The last one is the most divergent form and occupies also the most different microhabitat.

5. Ecomorphological guilds

Developmental modes in Madagascan amphibians can basically be classified into endotrophic and exotrophic. Two types of endotrophic development were assumed to exist in mantellids: direct development and nidicolous larvae, but in this work we can only confirm the presence of nidicolous larvae in *Gephyromantis*. Ten different ecomorphological guilds can be defined (Figure 5 and 6). The *(1)* generalized tadpoles with the typical oral disk containing all the usual components – keratinized teeth and jaw sheath, between two to eight upper (of which usually only one is continuous) and three lower (of which usually the first one is interrupted) labial tooth rows (LTR), medium sized papillae, and the presence of a dorsal gap of papillae – are found in *Aglyptodactylus*, *Boophis*, *Blommersia*, *Gephyromantis*, *Guibemantis*, *Laliostoma*, *Mantella*, *Mantidactylus*, *Spinomantis*, and *Tsingymantis*. The *(2)* adherent tadpoles – which are characterized by the presence of a dorsal gap of papillae, the ribbed state of the lower sheath, the rudimentary state or absence of the upper sheath, the presence of rather high number of small sized papillae, and the presence of seven to eight upper (of which three to four are continuous) and three uninterrupted lower LTR – are found in the *Boophis albipunctatus* and *Boophis mandraka* group. The *(3)* suctorial tadpoles – which are characterized by the absence of a dorsal gap of papillae, the ribbed state of the lower sheath, the always presence of the upper sheath, the presence of numerous small papillae, and the presence of eight upper (of which four being continuous) and

three uninterrupted lower LTR – are found in all *Boophis marojezensis*-like and *Boophis vittatus*. The carnivorous *(4)* tadpoles show a presence of a hypertrophied upper jaw sheath, two to three upper and one to three lower LTR, and elongated big papillae. They are only found in three species of *Gephyromantis* (subgenus *Phylacomantis*). Tadpoles characterized by *(5)* the reduction of the keratinization of the oral disk, two to three upper and three lower LTR (scattered for *Ochthomantis*), moderately sized papillae, and the presence of a dorsal gap of papillae are found in *Mantidactylus* (subgenera *Ochthomantis* and *Maitsomantis*) and *Boophis* (*B. majori* and *B. majori* [Ca 35 Glaw & Vences 2007]). Tadpoles characterized by *(6)* the reduction of the keratinization of the oral disk, the absence of labial teeth, and the presence of a dorsal gap of papillae, are found in *Mantidactylus* (subgenus *Ochthomantis*). Tadpoles characterized by *(7)* having three big thorn-shaped papillae-like structures in the place of the upper sheath, the absence of labial teeth, and the presence of many elongated and pointed papillae, are only found in *Mantidactylus majori* (subgenus *Ochthomantis*). Tadpoles characterized by *(8)* having many spike-like structures instead of jaw sheaths, the absence of papillae and upper LTR, and the presence of three lower LTR, are only found in *Mantidactylus* (*Hylobatrachus*). Tadpoles having *(9)* a commodious mouth opening characterized by loosing all the typical keratinized components of the oral disk are only found in *Boophis picturatus*. *(10)* Funnel-mouthed tadpoles characterized by an upward oriented umbelliform oral disk – that is shaped by an extended lower lip – usually without labial teeth and papillae are specific for *Mantidactylus*, subgenus *Chonomantis*.

6. Systematics – reverse taxonomy

To attain the objectives of this work, an accurate identification of the tadpoles is crucial. As most of the frog larvae were previously unknown, the use of DNA barcoding approach as a basal tool for determining the tadpole species was successfully applied in this work. DNA barcoding was based on a fragment of the mitochondrial 16S rRNA gene of the tadpoles compared to a near-complete database of sequences of adult Malagasy frog species. Identification was considered to be unequivocal when the tadpole sequence was 99–100% identical to an adult specimen from the same geographical region, and clearly less similar to all sequences from other species. In a first step, a divergent tadpole sequence was found first in *Mantidactylus* (subgenus *Ochthomantis*). As the corresponding tadpole is also morphologically divergent, we applied the 'reverse taxonomy' scheme by considering it as a confirmed candidate species. Later, most of the newly caught strongly rheophilous *Boophis* tadpoles had divergent sequences, so 12 candidate species were defined. Within those three were classified as confirmed candidate species as their molecular divergence could be confirmed by morphological divergence.

This work lead also into new insights of the systematics of the Mantellidae: *(1)* the systematic problem of *Mantidactylus femoralis* – a previously poorly defined species – is more or less resolved, and this species is now confirmed to occur over wide areas of eastern Madagascar; *(2)* the assignment of *M. mocquardi* to a species located in the northern central east of Madagascar is confirmed; and *(3)* the necessity of a revision of the *B. marojezensis*-like and *B. sambirano*-like species is also confirmed.

7. Perspective

This comprehensive data set that I have gathered now will allow many phylogenetic and evolutionary inferences to understand tadpole evolution in Madagascar. In total, 170 tadpoles belonging to the family of Mantellidae were studied using 119 variables (Appendix 3, Table 13). Analysis was performed with MrBayes to get a preliminary tree (Figure 8). A phylogenetic tree provided by Wollenberg and Vences (unpublished) based on three mitochondrial genes (16S, cyt b, co1) with the basal relationships further supported by several additional mitochondrial and nuclear genes was loaded into PAUP together with the character matrix of tadpole morphology for getting a tree topology (Figure 9), in which the branch lengths are therefore proportional to morphological change of tadpoles.

The morphological tree based on tadpole characters shows that *(1)* several genera and subgenera of mantellids can be supported by tadpole morphological characters: most species of *Boophis* grouped together, most species of *Spinomantis* grouped together, subgenus *Chonomantis* is supported, and the relationship between subgenera *Ochthomantis* and *Chonomantis* is supported. However there were also *(2)* tadpoles belonging to different species which are not phylogenetic sister species, grouped together due to morphological characters. A prime example is the one of *Boophis picturatus* which was placed within *Mantidactylus* (*Ochthomantis*). This indicates that these unrelated taxa show strong convergences in some aspects of their tadpole morphology.

Concerning the tree topology, the genus *Boophis* has many generalized tadpoles, but the *Boophis albipunctatus* group has adherent tadpoles which are really different from the basal ones. Therefore, their cluster has a long branch. The *Boophis microtympanum* group has also generalized tadpoles but the tadpoles of *Boophis williamsi* are morphologically very different. A similar example is also found in *Boophis majori* group. Due to its outstanding morphology, *Boophis picturatus* has the longest branch. This means that this species has the maximum morphological change which can be recognized through the oral disk structures. The subfamily of Mantellinae is also characterized by many morphological changes. The genus *Gephyromantis* contains some generalized tadpoles, but then it has also non-feeding and carnivorous tadpoles. The subgenus

Ochthomantis is characterized by the reduction and change in the oral disk of tadpoles. The subgenus *Chonomantis* has a totally different kind of tadpoles which are very similar to each other. The subgenus *Brygoomantis* is closely related to *Chonomantis* but it has generalized tadpoles. So a reversal needs to be assumed here, and therefore these tadpoles are clustered with a long branch.

This analysis shows already that there are two major instances of convergence in mantellid tadpoles: the first one is the reduction of the oral disk between the subfamily of Boophinae and Mantellinae, and the second one is the enlargement of the oral disk in different groups of *Boophis*.

A much more detailed and precise analysis of these data is planned for the next years and a perspective to better understand the relevance of tadpole morphological adaptations for the diversification of the Mantellidae.

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Chapter 2

The diversity of strongly rheophilous tadpoles of Malagasy tree frogs, genus Boophis and identification of new candidate species via larval DNA sequence and morphology.

This chapter will be submitted for publication as follows:

Randrianiaina RD, Strauß A, Glos J & Vences M. 2011. Diversity of the strongly rheophilous tadpoles of Malagasy tree frogs, genus *Boophis*, and identification of new candidate species via larval DNA sequence and morphology.

Abstract

New detailed morphological descriptions of strongly rheophilous tadpoles of the treefrog genus *Boophis*, data on habitat preference of these tadpoles in Ranomafana National Park, and their classification into ecomorphological guilds are provided in this study. A total of twenty-two tadpoles determined via DNA barcoding are described, within fourteen are newly described including twelve candidate species. As most of these tadpoles have a rather similar morphology, they are easily classified into two different groups: the first group is characterized by the presence of a dorsal gap of papillae and the absence of an upper jaw sheath in some species. It includes the tadpoles of the *B. albipuncatus* group (*B. schuboeae*, *B. ankaratra*, *B. albipunctatus*, *B. sibilans*, and *B. luciae*) and *B. mandraka* group (*B. sambirano*, *B. mandraka* [Ca38 Vieites et al. 2009], *B. mandraka* [Ca46 ZCMV 3479], *B. sambirano* [Ca47 ZCMV 13105], *B. sambirano* [Ca48 ZCMV 13109], *B. sambirano* [Ca49 ZCMV 13155], and *B. sambirano* [Ca50 ZCMV 13172]). The second group includes all *B. marojezensis*-like tadpoles (*B. marojezensis*, *B. marojezensis* [Ca25 Vieites et al. 2009], *B. marojezensis* [Ca26 Vieites et al. 2009], *B. marojezensis* [Ca51 ZCMV 3691], *B. marojezensis* [Ca52 ZCMV 13168], and *B. marojezensis* [Ca53 ZCMV 13200]) and *B. vittatus* which have an enlarged oral disk without any dorsal gap. The first group is considered as "adherent" as they inhabit fast-running waters and their oral disk is commonly to continuously attached to the rocky substrate to keep their position in the water current. The second group is considered as "suctorial" as they inhabit fast-running waters and their oral disk is always countinously attached to the substrate. An ecological analysis of the tadpoles of *B. luciae*, *B. schuboeae* and *B. marojezensis* [Ca51] from Ranomafana National Park does not show a clear preference of these tadpoles to the fast flowing sections of the stream, although it is obvious that all tadpoles of this study are caught in this habitat.

Key words: Amphibia, Anura, Mantellidae, *Boophis*, larval morphology, oral disk, suctorial, adherent, adaptation, evolution, ecology

Introduction

Seventy-two nominal species and over 25 candidate species of *Boophis* are currently known (Vieites et al. 2009; Vallan et al. 2010; Glaw et al. 2010; Vences et al. 2010a, b), but tadpoles have only been described for 46 out of these (*e.g.*, Blommers-Schlösser 1979; Thomas et al. 2005; Grosjean et al. 2006; Raharivololoniaina et al. 2006; Altig & McDiarmid 2006; Glos et al. 2007;

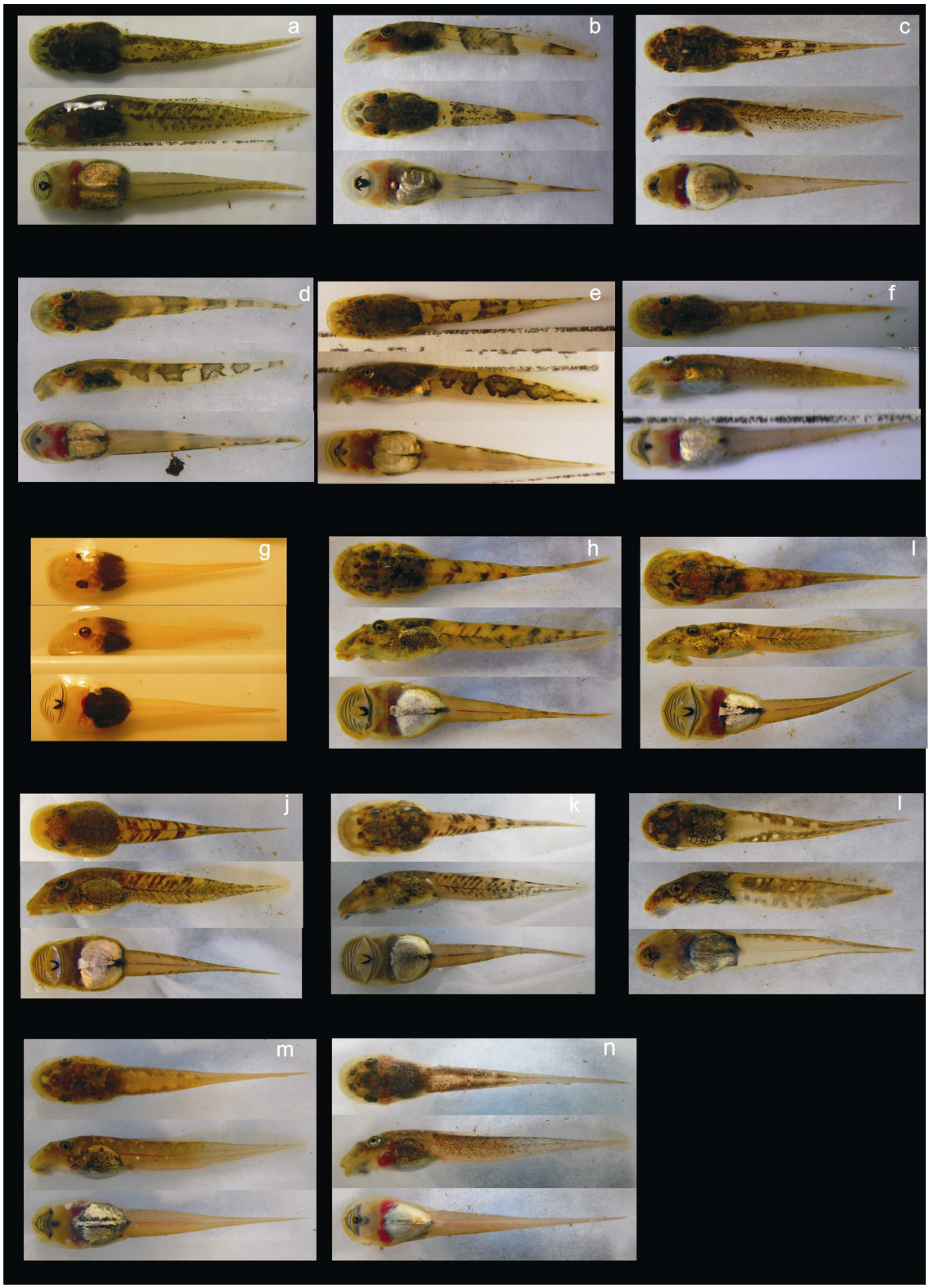

Figure 1. Coloration in life of strongly rheophilous tadpoles (dorsal, lateral and ventral views): **a** – *B. ankaratra* (ZCMV 4917 – ZSM 876/2007); **b** – *B. schuboeae* (T 09/980 – 743/2008); **c** – *B. andohahela* (T 09/0273- ZSM 282/2009); **d** – *B. sibilans* (ZCMV 11548 - to be catalogued in ZSM); **e** – *B. luciae* (ZCMV 11548 - to be catalogued in ZSM); **f** – *B. albipunctatus* (ZCMV 4946 – ZSM 82/2008); **g** – *B. mandraka* [Ca38] (ZCMV 4261 - ZSM 456/2007); **h** – *B. sambirano* [Ca47] (ZCMV 13105 - ZSM 482/2010); **i** – *B. sambirano* [Ca48] (ZCMV 13109 - ZSM 486/2010); **j** – *B. sambirano* [Ca49] (ZCMV 13155 - ZSM 528/2010); **k** – *B. sambirano* [Ca50] (ZCMV 13172 - ZSM 545/2010); **l** – *B. marojezensis* [Ca51] (ZCMV 13550 - ZSM 721/2010); **m** – *B. marojezensis* [Ca52] (ZCMV 13168 - ZSM 541/2010); **n** – *B. marojezensis* [Ca53] (ZCMV 132000 - ZSM 573/2010)

Schmidt et al. 2008; Randrianiaina et al. 2009a, b; and Rasolonjatovo et al. 2010). However, compared to many other Malagasy anuran groups, the larval stages of *Boophis* are quite well known, possibly because they are relatively easy to find in rainforest streams (*e.g.*, Strauß et al. 2010) and even sometimes outside the forest (Figure 26). The strongly rheophilous tadpoles of Malagasy *Boophis* frogs have been known since the work of Blommers-Schlösser (1979) in which tadpoles having this morphology were described and assigned to *Boophis majori, B. erythrodactylus*, *B. mandraka*, and *Boophis* sp.. The tadpoles assigned by this author to *Boophis majori* belong probably to *B. marojezensis*, and the identity of tadpoles assigned to *B. erythrodactylus* remains uncertain, because this species belongs to a species group which has generalized tadpoles. Raharivololoniaina et al. (2006) described the tadpoles of *B. marojezensis* and *B. sibilans* from Andasibe. Glos et al. (2007) described *B. schuboeae* tadpoles from Ranomafana and *B. ankaratra* tadpoles from Andringitra, and Thomas et al. (2006) described *B. andohahela* tadpoles from Ranomafana. Rasolonjatovo et al. (2010) described *B. englaenderi*, *B. luciae*, and *B. vittatus*.

In this study, morphological data on twenty-two strongly rheophilous tadpoles are provided, of which fourteen are newly described: *B. albipunctatus*, *B. englaenderi* [Ca45 Vieites et al. 2009], *B. sambirano*, *B. mandraka* [Ca38 Vieites et al. 2009], *B. mandraka* [Ca46 ZCMV 3479], *B. sambirano* [Ca47 ZCMV 13105], *B. sambirano* [Ca48 ZCMV 13109], *B. sambirano* [Ca49 ZCMV 13155], *B. sambirano* [Ca50 ZCMV 13172], *B. marojezensis* [Ca25 Vieites et al. 2009], *B. marojezensis* [Ca26 Vieites et al. 2009], *B. marojezensis* [Ca51 ZCMV 3691], *Boophis marojezensis* [Ca52 ZCMV 13168], and *Boophis marojezensis* [Ca53 ZCMV 13200]. All these strongly rheophilous tadpoles are characterized by their "streamlined" (*i.e.*, elongated, narrow and flat) body form, their wide oral disk containing many tooth rows in which all posterior rows are uninterrupted, their completely keratinized jaw sheath, in which the lower one is always "ribbed" and the upper one can be absent in some species, and many small rounded papillae with or without a dorsal gap. The absence of many of these characteristics in *B. williamsi* tadpoles (Blommers-Schlösser 1979 and Schmidt et al. 2008) is the criteria of excluding them from the present study.

In the context of grouping Malagasy tadpoles into different ecomorphological guilds, Raharivololoniaina et al. (2006) have classified some *Boophis* tadpoles according to their morphological traits. However, for the appropriate definition of ecomorphological guilds, it is necessary to include real ecological data. Therefore, an ecological analysis of three most abundant strongly rheophilous tadpoles (*B. luciae*, *B. marojezensis* [Ca51], and *B. andohaela*) was performed in 30 streams in Ranomafana National Park to verify if the typical morphological characteristics of these tadpoles are indeed adaptations to their fast-running stream habitat, as it has been predicted by Blommers-Schlösser (1979).

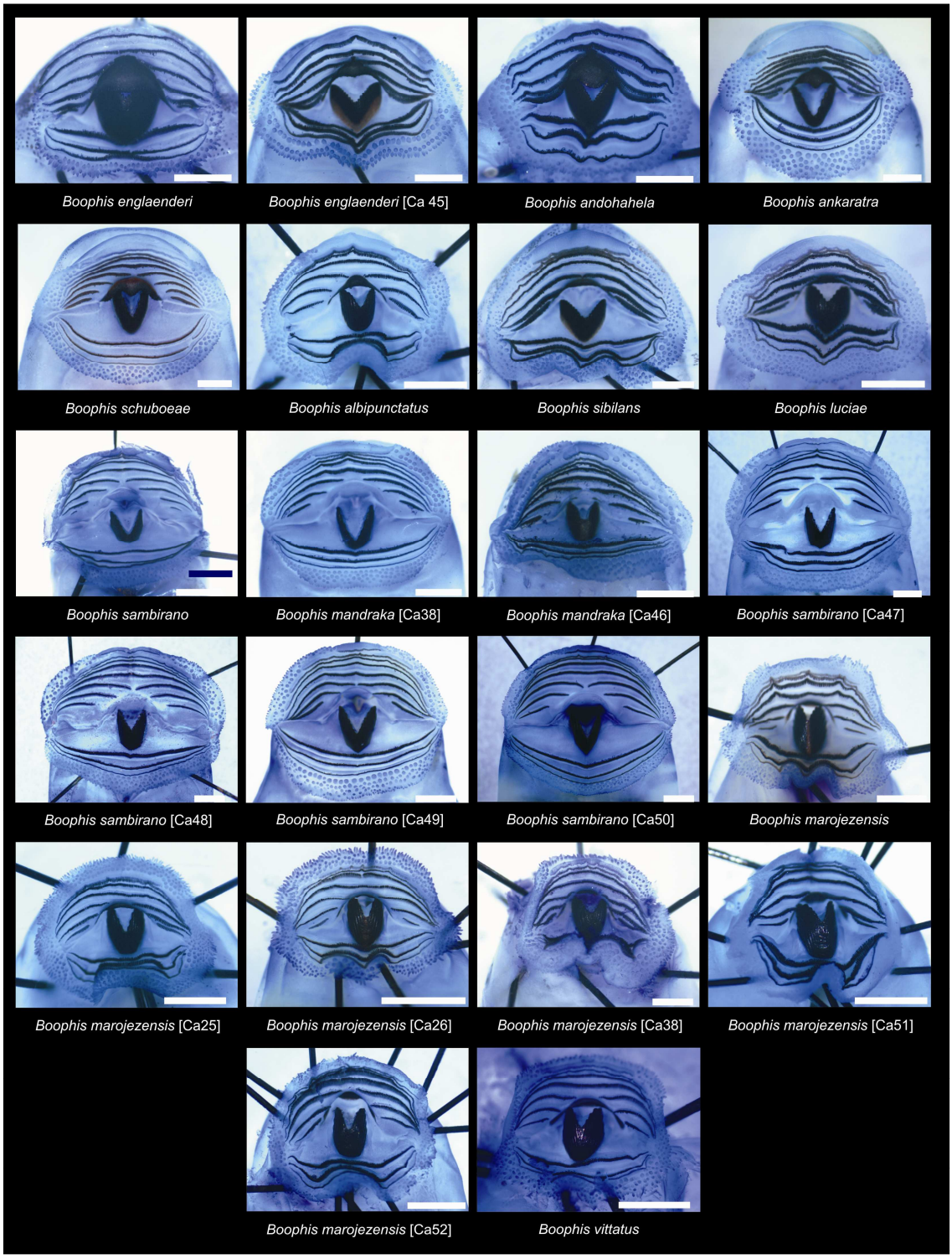

Figure 2. Pictures of the oral disks of the voucher specimens.

Using DNA barcoding to identify these poorly known amphibian larvae at species level has progressed tremendously within the last years (*e.g.*, Thomas et al. 2005) and has already been fruitful by inducing a so called "reverse taxonomy" in this vertebrate group (Randrianiaina et al. 2011). This study confirms this progress by discovering 12 candidate species via tadpole DNA sequences and morphology.

Materials and methods

1. Morphological study of tadpoles

Tadpoles were collected by different kind of nets having mesh sizes from 2 to 5 mm, depending on the size of the streams, the strength of the current and the type of substrate. They were euthanized by immersion in chlorobutanol solution, and immediately sorted into homogeneous series based on morphological characters. From each series one specimen was selected and a tissue sample from its tail musculature or fin taken and preserved in 99% ethanol. This specimen is here called "DNA voucher". All detailed morphological tadpole characterizations and drawings are based on this DNA voucher, whereas variation is described based on further specimens of the series. After tissue collection, all specimens were preserved in 5% formalin or 70% ethanol. Specimens were deposited in the Zoologische Staatssammlung München, Germany (ZSM). When referring to voucher specimens the original field numbers (FG/MV, FGZC, T, and ZCMV) are usually provided together with the final ZSM catalogue numbers. Tadpoles studied in this paper are summarized in the Appendix 2 (Table 1) including data concerning the site and its coordinates, the date of the capture and the collectors.

For detailed morphological examination, especially to determine developmental stages and assess characters of the oral disk, preserved tadpoles were stained slightly with methylene blue. Tadpoles were examined under water and few drops of methylene blue were applied to the oral disk, hind limb, spiracle, narial opening and vent tube for having a better view of their structures. Developmental stages are determined following Gosner (1960).

Morphological description, measurements and drawings were done on digital pictures of the preserved tadpoles taken with a stereomicroscope Zeiss Discovery V12 connected to a computer, following landmarks, terminology and definitions of Altig & McDiarmid (1999a) and Randrianiaina et al. (2011), except that we predominantly use the term keratodonts instead of labial teeth. The formula of keratodonts (= labial tooth row formula, LTRF) is given according to Altig & McDiarmid (1999a). Drawings and photographs of the preserved tadpoles are shown in Appendix. Comparing measurements, we consider them as "almost equal" if ratios of the mea-

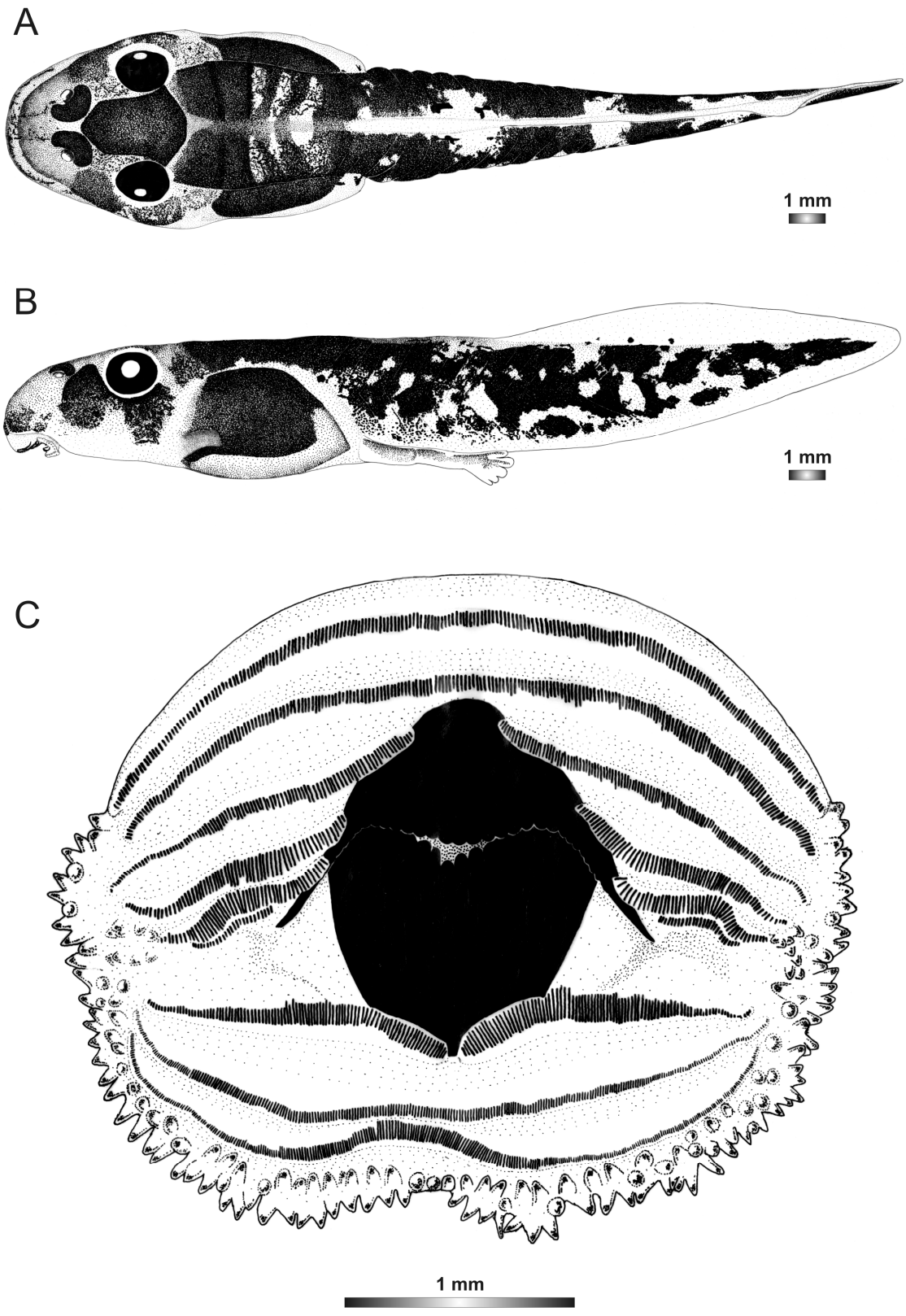

Figure 3. Drawings of the preserved DNA voucher tadpole of *Boophis englaenderi* (FGZC 2244 - ZSM 623/2008): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

sured values are 95–96% or 104–105%, "equal" if they are in the range 97-103%, as almost "in the middle" if they are in the range 45-46% or 54-55% and "in the middle" if they are in the range 47-53% (Randrianiaina et al. 2011).

The following abbreviations are: A_1 (first upper keratodont row), A_2 (second upper keratodont row), A_{2gap} (medial gap in A_2), A_3 (third upper keratodont row), A_4 (fourth upper keratodont row), A_5 (fifth upper keratodont row), A_6 (sixth upper keratodont row), A_7 (seventh upper keratodont row), A_8 (eighth upper keratodont row), $A_{1\text{-}8\ den}$ (density of the keratodonts in row $A_{1\text{-}8}$), $A_{18\ len}$ (length of $A_{1\text{-}8}$), $A_{1\text{-}8\ num}$ (number of keratodonts in $A_{1\text{-}8}$), BH (maximal body height), BL (body length), BW (maximal body width), DF (dorsal fin height at midtail), DG (size of the dorsal gap of marginal papillae), DMTH (distance of maximal tail height from the tail-body junction), ED (eye diameter), EH (eyes height – measured from the lower curve of the belly), HAB (height of the point where the axis of the tail myotomes contacts the body – measured from the lower curve of the belly), IND (inter-narial distance – measured in the middle), IOD (inter-orbital distance – measured in the middle), JW (maximal jaw sheath width), MC (medial convexity of the upper sheath), MCL (length of the medial convexity of the upper sheath), MP (marginal papillae), MTH (maximal tail height), ND (naris diameter), NH (naris height – measured from the lower curve of the belly), NP (naris-pupil distance), OD (oral disk), ODW (maximum oral disk width), P_1 (first lower keratodont row), P_2 (second lower keratodont row), P_3 (third lower keratodont row), $P_{1\text{-}3\ den}$ (density of the keratodonts in $P_{1\text{-}3}$), $P_{1\text{-}3\ len}$ (length of $P_{1\text{-}3}$), $P_{1\text{-}3\ num}$ (number of keratodonts in $P_{1\text{-}3}$), RN (rostro-narial distance), PCA (Principal Component Analysis), SBH (distance between snout and the point of maximal body height), SBW (distance between snout and the point of maximal body width), SE (snout-eye distance), SH (spiracle height – measured from the lower curve of the belly), SL (spiracle length), SMP (submarginal papillae), SS (snout-spiracle distance), SV (spiracle-vent distance), TAL (tail length), TH (tail height at the beginning of the tail), THM (tail height at midtail), Thorn-pap (thorn-shaped papillae), TL (total length), TMH (tail muscle height at the beginning of the tail), TMHM (tail muscle height at midtail), TMW (tail muscle width at the beginning of the tail), LR (number of the lower rows of keratodonts), UR (number of the upper rows of keratodonts), VF (ventral fin height at midtail), VG (size of the ventral gap of marginal papillae), VL (vent tube length).

2. Molecular analyses

DNA barcoding was based on a fragment of the mitochondrial 16S rRNA gene, which is known to be sufficiently variable among species of Malagasy frogs (Vences et al. 2005). We amplified a fragment of ca. 550 bp using primers 16Sar-L and 16Sbr-H from Palumbi et al. (1991), or a shorter fragment of ca. 400 bp using the newly developed specific mantellid primers

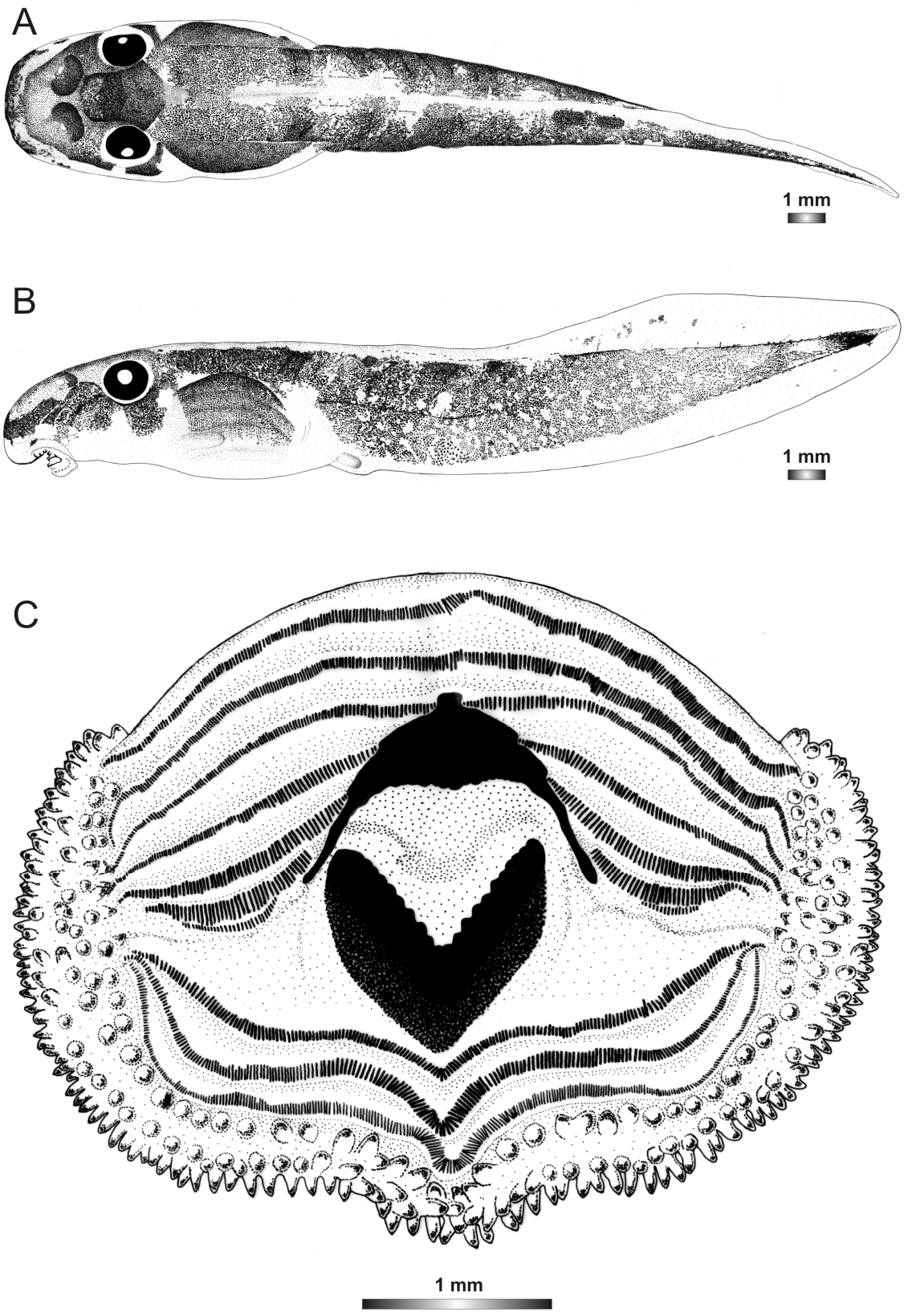

Figure 4. Drawings of the preserved DNA voucher tadpole of *B. englaenderi* [Ca45] (FGZC 2957 - ZSM 1632/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

16S-Frog-L1 (CAT AAT CAC TTG TTC TTT AAA) and 16S-Frog-H1 (GAT CCA ACA TCG AGG TCG). PCR was carried out with standard protocols (Vences et al. 2005) and sequences resolved on automated sequencers. Sequences were preliminarily identified using BLAST searches against a near-complete database of sequences of adult Malagasy frog species. Results were subsequently verified by manually aligning and comparing sequences to the closest hits in the data base. Identification was considered to be unequivocal when the tadpole sequence was 99–100% identical to an adult specimen from the same geographical region, and clearly less similar to all sequences from other species. When no identity with adult specimens was found and divergence was >3% we considered the corresponding tadpoles to belong to additional candidate species, a situation that arose in a single case. DNA sequences were deposited in Genbank (accession numbers #####-##### to be added upon manuscript acceptance).

Candidate species nomenclature followed the scheme developed by Padial et al. (2010). We use the binomial species name of the closely related species, followed in square by the abbreviation "Ca" with an attached numerical code referring to the particular candidate species, and terminating with the author name and the year of publication of the article in which the lineage was first discovered for few species, but with the original field number for many of them in the beginning, and we replaced the field number by the GenBank accession number of the sequence when the sequence was submitted to Genbank. Further in the text, we abbreviate the candidate species name just by using the binomial species name followed in square brackets by the abbreviation "Ca" with an attached numerical code referring to the candidate species.

3. Ecological study of tadpoles

Within a study on stream tadpole communities in Ranomafana National Park (RNP) in the south eastern escarpment of Madagascar, 33 stream sections have been exhaustively sampled for tadpoles. Each section spanned 30 m and the sampling process was separated for all available microhabitats within the section. These microhabitats were predefined subject to underground substrate (rock, gravel, leaves, sand) as well as separately by the stream velocity categories "fast" (obviously running) and "slow" (almost stagnant). Habitat variables were recorded at two spatial levels: *(1)* habitat variables of possible importance for breeding site (stream) choice of frog species and *(2)* proportion of microhabitats available within the streams.

We used data from this study for an exemplary analysis of breeding site choice and microhabitat use of syntopic species of strongly rheophilous tadpoles. To identify the habitat variables of the stream and the surrounding forest that may be important for breeding site choice, we performed a principal component analysis (PCA) and plotted species according to their inci-

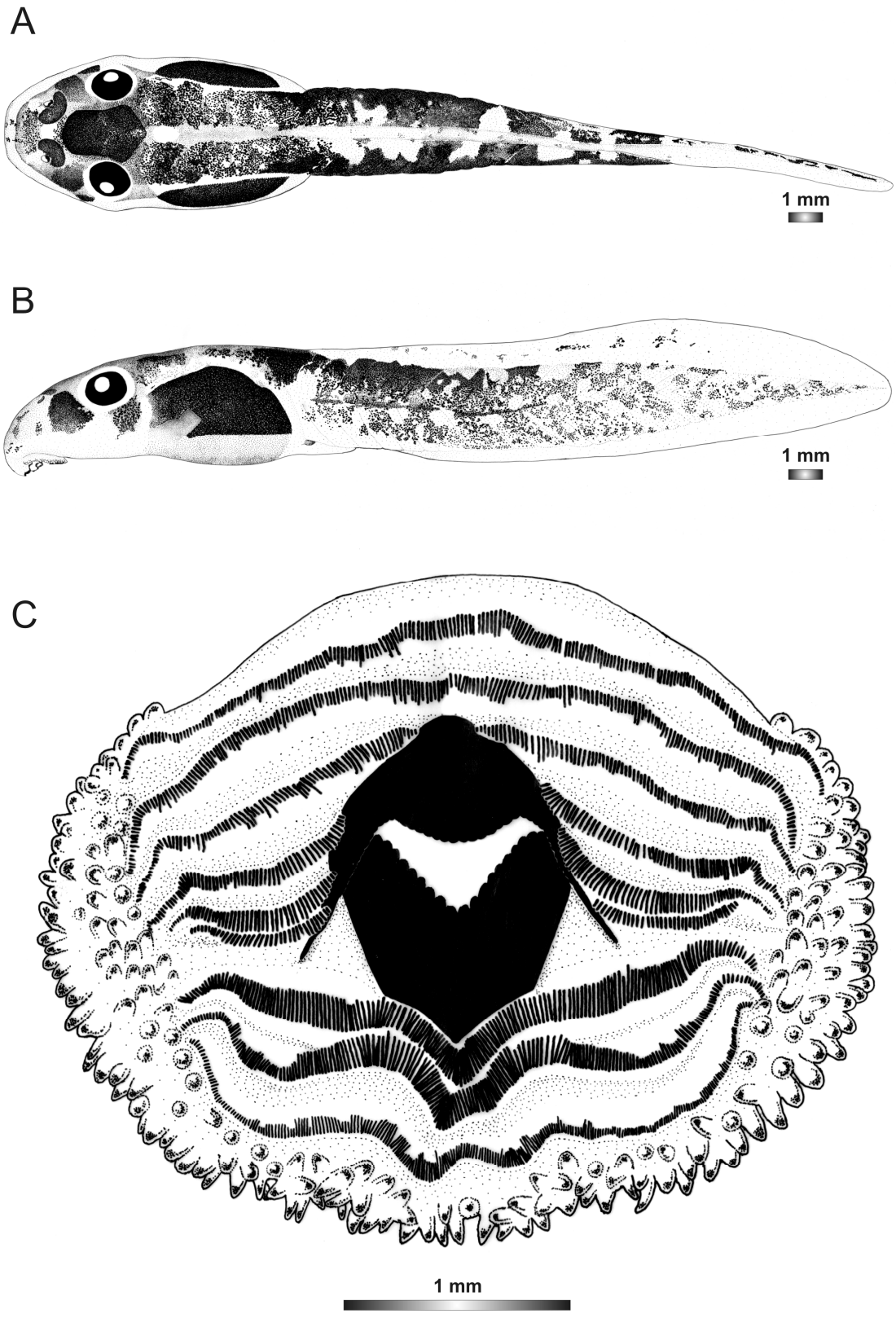

Figure 5. Drawings of the preserved DNA voucher tadpole of *Boophis andohahela* (T 2007-428 - ZSM 998/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

dence as supplementary variables in the PCA biplot. For PCA, we used all ten habitat variables of all 33 streams sampled during the tadpole community study. PCA was run on the correlation matrix in order to standardize for the influence of unequal variance. To evaluate data outliers and linear interdependence of variables, box-plots and pair-plots (Zuur et al. 2007) were used. As PCA requires multinormality of data, box-cox-power-transformations (Box & Cox 1964) were applied when necessary. The number of meaningful PCs was estimated by a scree plot (Zuur et al. 2007). PCA and correlation with species incidence was evaluated using the dimdesc function in package FactoMineR (Lê et al. 2008).

To analyse the use microhabitats within streams, we first used raw data graphing to display the species specific distribution between microhabitats. In order to quantify true preferences for microhabitats, Ivlev's electivity index (E, Ivlev 1961) was calculated for each strongly rheophilous *Boophis* species occurring in RNP. E is defined as E=(r-p)/(r+p) with r being the proportions of the microhabitats used and p the proportion of microhabitats available. To test whether the E values differ for the single species, a factorial ANOVA was run with E as dependent variable and the factors "microhabitat" and "species" as independent variables. This provides information whether E is different for the different microhabitats, whether E differs between species, and, if interactions could be included in model, whether the effect of the one factor depends on the level of the other factor. To avoid possible overparameterisation caused by large numbers of interactions (Crawley 2007), we removed the interaction term from the model and performed ANOVAs of subsets of the data to closer evaluate differences in preferences between species within specific microhabitats (interactions). Only the three abundant species were included in this analysis. Also, for each species only streams with at least eight specimens of the respective species were included in the analysis to reduce the influence of many high avoidance values due to a general low number of tadpoles in a stream.

Statistical analysis were performed in R 2.9.2 (R Development Core Team 2009) including libraries car (Fox et al. 2008) and FactoMineR (Lê et al. 2008).

Results

1. Tadpole descriptions

This part include just a brief account of mainly one characteristic species per species group, and brief account for all other species and candidate species emphasizing the difference that they show to other species belonging to the same group. Detailed descriptions and assessment of variation are found in the descriptions in the Appendix 1.

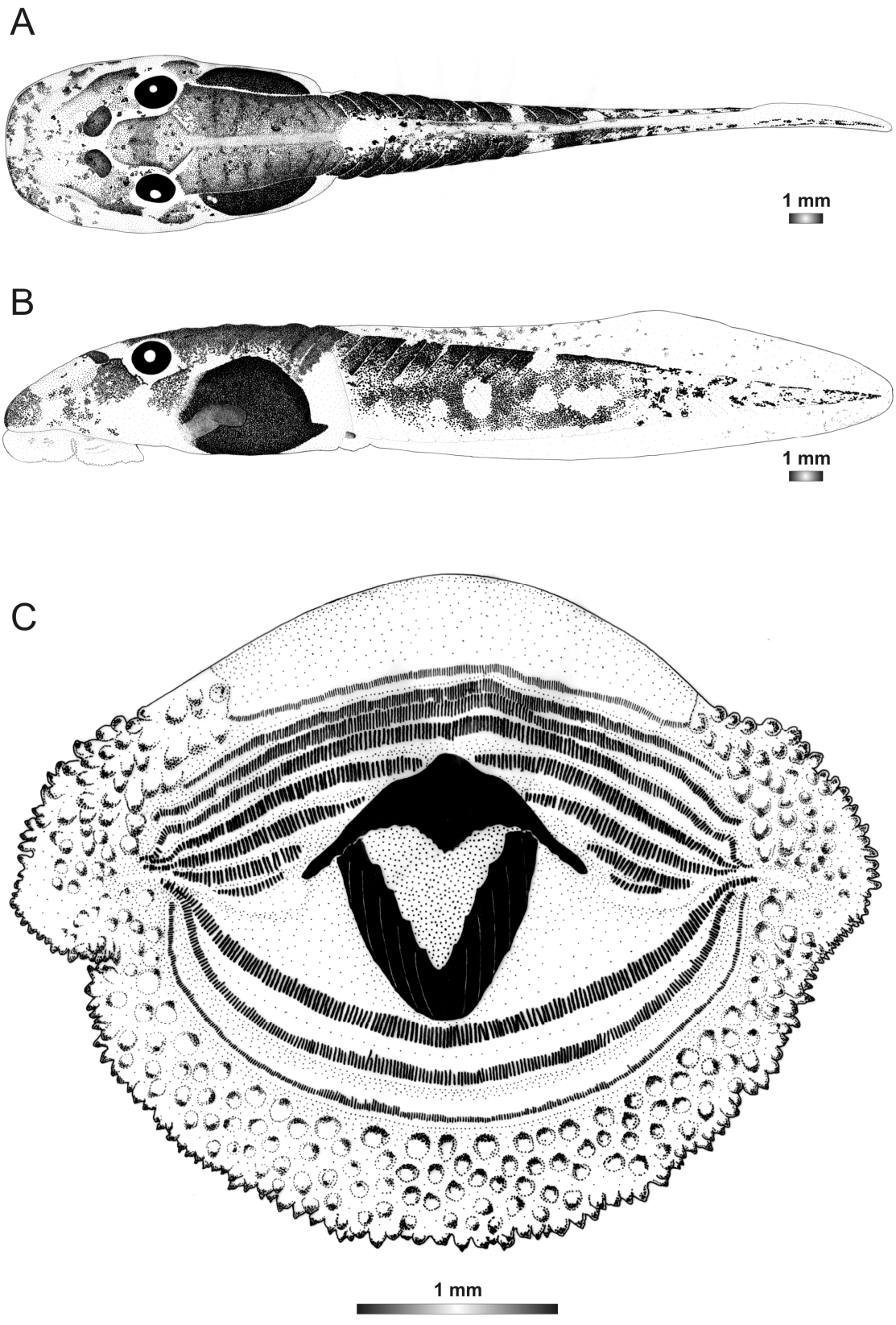

Figure 6. Drawings of the preserved DNA voucher tadpole of *Boophis ankaratra* (ZCMV 4917 - ZSM 876/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

Boophis luteus group

This group is characterized by tadpoles having a generalized oral disk without lateral emargination and ventral gap of papillae, but with a wide to very wide dorsal gap is. The anterior margin of the oral disk is a continuation of the snout. Usually a single (the first) uninterrupted upper tooth row and an interrupted first lower row are present, except the three species described herein. The jaw sheaths are very strong with smooth surface and completely or partially keratinized in some species. The upper sheath is always provided by a medial convexity. The dorsolateral glands are absent.

Boophis englaenderi Glaw & Vences 1994

Morphological data were assessed in one tadpole (Figures 2 and 3) in developmental stage 36 (Field number FGZC 2244; ZSM 623/2008, BL 11.8 mm, TL 25.4 mm, accession number to be added upon manuscript acceptance) from Marojejy National Park. The 16S rDNA sequence of this specimen was 99.5% identical to a reference sequence of an adult *B. englaenderi* (accession FJ559124) from Marojejy.

The tadpoles of this species have an elliptical body, a flatly rounded snout in dorsal view and a short tail. The distance between eyes is wide and nares are very large and round, positioned very high dorsally, situated nearer to snout than to eye and at eye level. The oral disk is characterized by having two uninterrupted upper and one interrupted lower tooth rows giving the LTRF is 6(3-6)/3(1). The upper jaw sheath is totally keratinized with rounded serrations, moderately wide with a very short widely rounded medial convexity. The lower sheath is V-shaped, completely keratinized, and partially hidden by the upper one. Both jaw sheaths are with smooth surface.

In preservative, the tadpole is generally dark brown. Dark brown spots condensed to form a hexagonal mark above the neocranium; a dark semicircular patch situated behind each narial opening and dark patches between the vertebral area and the abdominal region are present. The snout is spotted. The transversal lines between the vertebral area and the abdominal region are perceivable which make the domino-like structure on this area noticeable. The dorsal part of the tail muscle has five dark brown and four light alternating bands. The prominent dark brown band is the extension of the patches between the vertebral area and the abdominal region. The myosepta are visible on the dorsal part of the tail. Laterally, the jugal area is covered by dense dark brown patches and the dorsolateral part of flank is identical to the dorsal pattern; the ventrolateral part is pale and the abdominal region is very dark leaving an opaque discernible spiracle. Ventrally, oral disk, gular and branchial regions are pale; the venter is more or less trans-

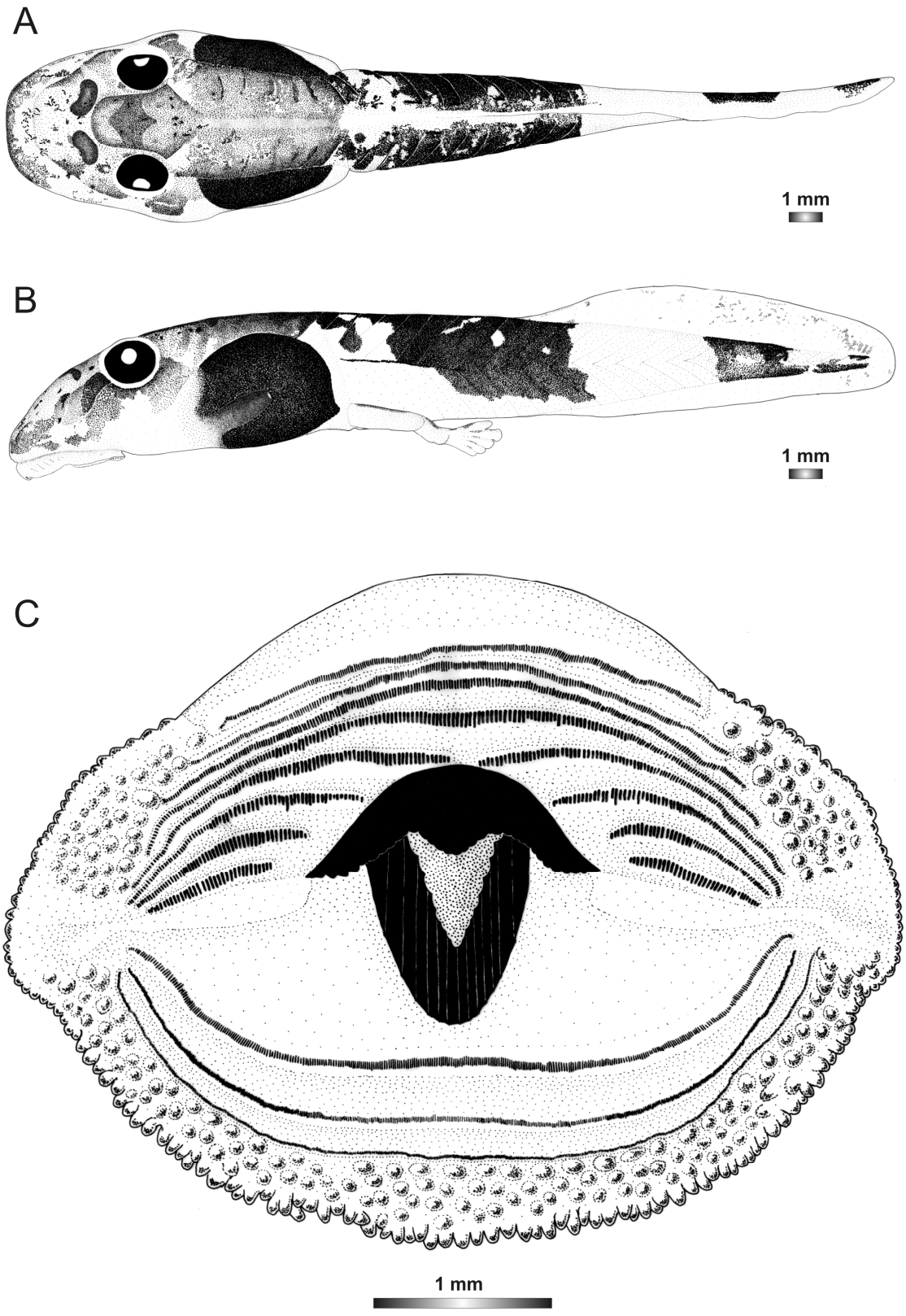

Figure 7. Drawings of the preserved DNA voucher tadpole of *Boophis schuboeae* (FG/MV 2003-1800 - ZSM 978/2004): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

parent and the intestinal coils are perceptible with a regularly spiral shaped. The tail musculature is pale and covered by dark brown spots which condense to form reticulations. Fins are transparent, with few brown spots on the dorsal fin and the ventral fin is free from pigment.

Boophis englaenderi [Ca45 FGZC 2257]

Morphological data were assessed in one tadpole (Figures 2 and 4) in developmental stage 30 (Field number FGZC 2257, ZSM 1632/2007, BL 10.5 mm, TL 29.5 mm, accession number to be added upon manuscript acceptance) from Marojejy National Park. The 16S rDNA sequence of this specimen was 94% identical to a reference sequence of an adult *B. englaenderi* (accession AY848474) from Ilampy. Nine other voucher specimens agree in morphology with the voucher specimen described herein.

The external morphology of this tadpole has a very close similarity with those of *B. englaenderi*, except that it has much longer tail, TAL/BL 183% *vs.* 153% and a lighter pigmentation. The difference between the two tadpoles is clearly shown in the oral disk structure. It is bulged laterally, has one more interrupted upper tooth row and a first uninterrupted lower row giving the tooth row formula LTRF 7(3-7)/3 *vs.* 6(3-6)/3(1). The number of papillae is more than those of *B englaenderi* with 175 marginal papillae *vs.* 128 and 94 submaginal papillae *vs.* 33, although this tadpole is still in developmental stage inferior to *B. englaenderi*. The submarginal papillae are complete on the lower labium. This tadpole is also characterized by a light brown coloration in preservative. The jugal area is covered by scarce light brown patches, and the tail musculature is covered by light brown spots which group in some area to form patches or sparse reticulations. The intestinal coils are visible. The examination of nine other voucher specimens confirms the difference with *B. englaenderi*.

Boophis andohahela Andreone, Nincheri & Piazza 1995

Morphological data were assessed in one tadpole (Figures 2 and 5) in developmental stage 26 (Field number T 428; ZSM 998/2007, BL 11.8 mm, TL 25.4 mm, accession number to be added upon manuscript acceptance) from Ranomafana National Park. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult *B. andohahela* (accession AY848456) from the same locality. Five out of six other voucher specimens have the morphological characteristics of this species, whereas one tadpole has a difference in the oral disk configuration.

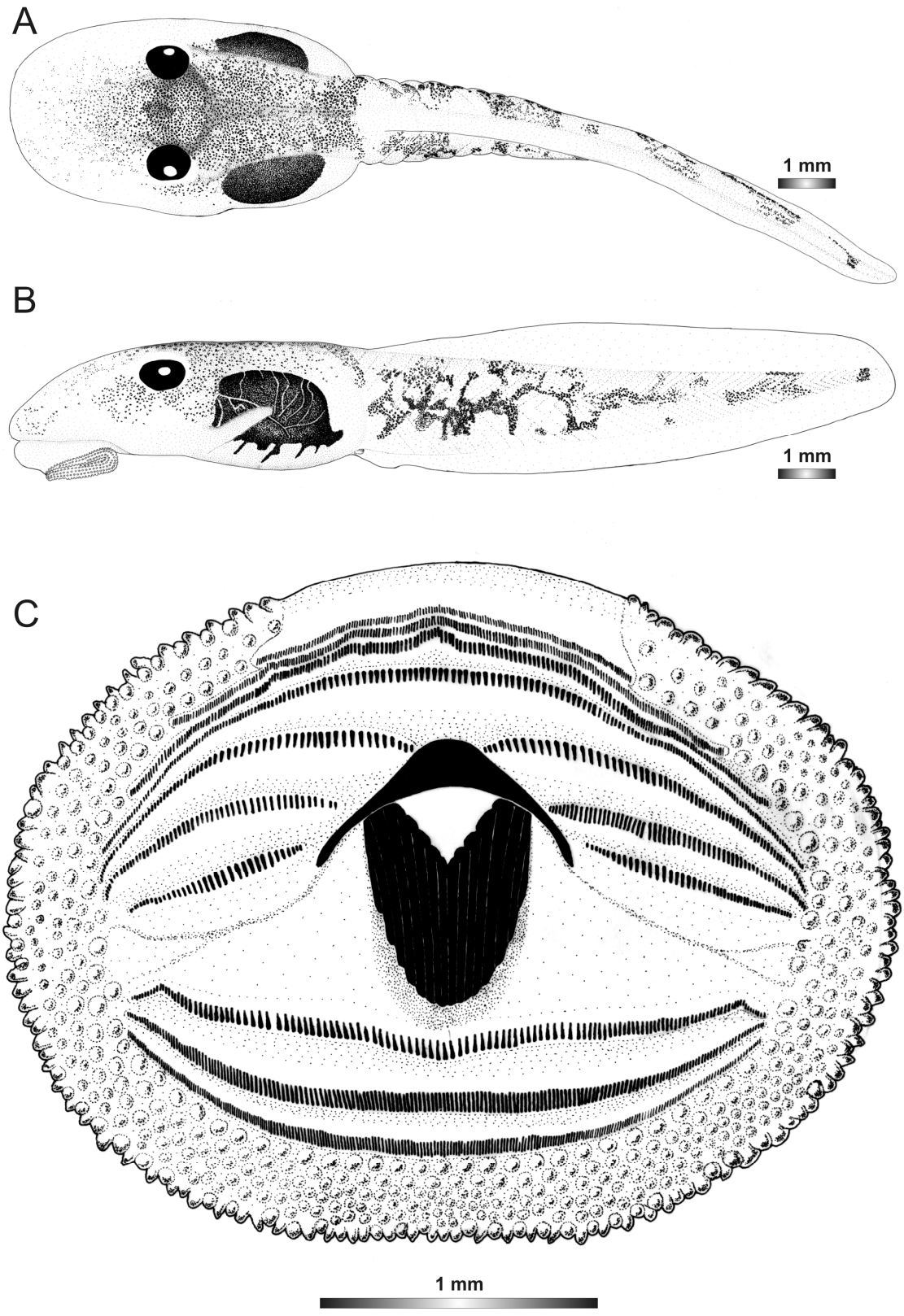

Figure 8. Drawings of the preserved DNA voucher tadpole of *Boophis albipunctatus* (ZCMV 4946 - ZSM 82/2008): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

The general morphology of this tadpole looks like the same with *B. englaenderi* and *B. englaenderi* [Ca45], but it is characterized by the presence of a white patch behind the hexagonal mark in life and even in preservative. The non visibility of its intestinal coils is shared with *B. englaenderi*. The LTRF 6(3-6)/3 is identical to some specimens of *B. englaenderi* [Ca45] but differs from *B. englaenderi*, on the other hand, the absence of papillae on the ventral area of the oral disk is similar to that of *B. englaenderi*. The oral disk of this tadpole has a slightly developed lateral bulge.

***Boophis albipunctatus* group**

This group is characterized by tadpoles having an enlarged oral disk without lateral emargination (but bulged laterally for some species) and ventral gap of marginal papillae. The dorsal gap is moderately wide. The anterior margin of the oral disk is separated by a deep crevice to the snout; *i.e.*, the entire margin is free from the snout. The upper labium has always four uninterrupted upper tooth rows, but the interrupted tooth rows can be three or four and the three lower rows are always uninterrupted giving the LTRF 8(5-8)/3 and 7(5-7)/3. The jaw sheaths are moderately strong and completely keratinized. The upper sheath is provided by medial convexity in few species. The lower sheath is U or V-shaped and ribbed. The dorsolateral glands are present.

Boophis ankaratra Andreone 1993

Morphological data were assessed in one tadpole (Figures 2 and 6) in developmental stage 28 (Field number ZCMV 4917, ZSM 876/2007, BL 11.3 mm, TL 25.5 mm, accession number to be added upon manuscript acceptance) from Ranomafana National Park. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult *B. Ankaratra* (accession AJ315909) from Mandraka. Two other voucher specimens possess the typical morphological characters of the species.

This tadpole can be differentiated with *B. luteus* group tadpoles by the general state of the oral disk. It is characterized by an enlarged and laterally bulged oral disk. There is a double row of marginal papillae interrupted by a moderately wide dorsal gap. Papillae are short, small, conical with protuberance, and rounded tipped. There are 148 and 190 marginal and submarginal papillae, respectively. The LTRF is 8(5-8)/3 and A_1 is moderately long. The jaw sheaths are moderately strong and totally keratinized. The upper sheath is provided by a short narrowly pointed medial convexity. The lower sheath is U-shaped, ribbed, higher than wide, and partially hidden by the upper one.

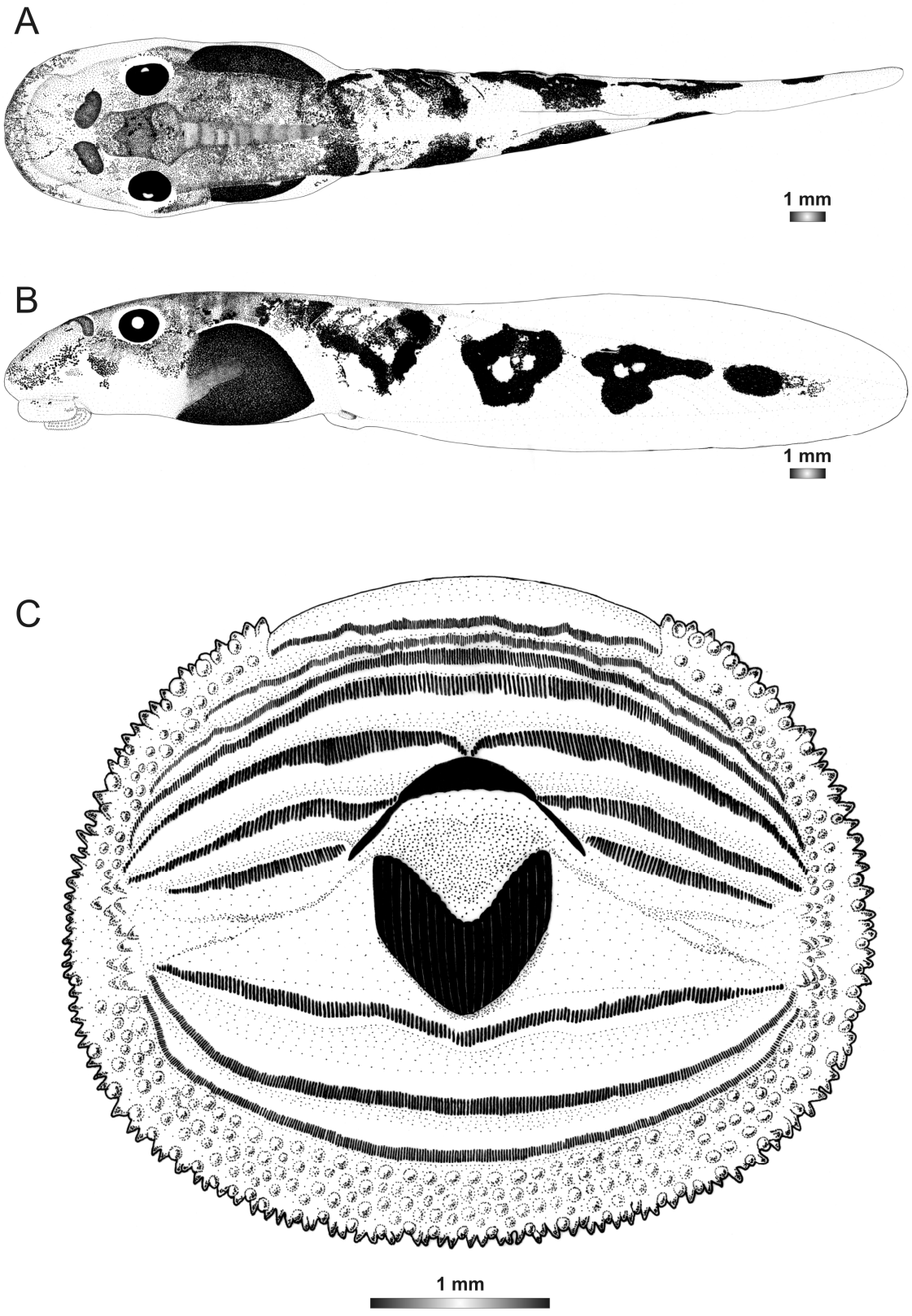

Figure 9. Drawings of the preserved DNA voucher tadpole of *Boophis sibilans* (FGZC 2956 - ZSM 1631/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

In life this tadpole is generally dark brown. Dorsally, body and tail covered by dense brown spots. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. The domino-like structures between the vertebral area and the abdominal region are recognizable. Few irregularly dark blotches and silvery spots scatter on the skin. Laterally, jugal area covered by dense brown patches and the abdominal region is very dark leaving a transparent noticeable spiracle. The tail musculature is yellowish and covered by sparse brown spots which coalesced to form patches. Their density diminishes toward the tail tip. Fins are transparent with few brown blotches on the dorsal fin and the ventral fin is almost free from pigment. Ventrally, intestinal coils are not visible. In preservative, the tadpole concord with the upper description except that it is paler and the silver tissue which covers the heart and the venter becomes whitish.

Boophis schuboeae Glaw & Vences 2002

Morphological data were assessed in one tadpole (Figures 2 and 7) in developmental stage 36 (Field number FGMV 2002-1800, ZSM 978/2004, BL 12.1 mm, TL 25.5 mm, accession number to be added upon manuscript acceptance) from Ranomafana National Park. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult *B. schuboeae* (accession AJ315912) from the same locality. Six other voucher specimens from the same locality show the typical coloration pattern and oral disk configuration of the species.

The oral disk of the tadpoles belonging to this species is identical to those of *B. ankaratra*, except that it has a rather smaller and lower number of papillae and the lateral area where the oral disk folds is free from submarginal papillae. They are easily to distinguish by their particular coloration pattern. They are characterized by the presence of up to for light and three alternating bands on the tail musculature. In life, the distal part of the tail is sometimes with a contrasting orange coloration. Generally dorsal and ventral fins originate on the tail musculature for *B. schuboeae*, although it is commonly on the body-tail junction for *B. ankaratra*.

Boophis albipunctatus Glaw & Thiesmeier 1993

Morphological data were assessed in one tadpole (Figures 2 and 8) in developmental stage 25 (Field number ZCMV 4946, ZSM 82/2008, BL 7.5 mm, TL 15.5 mm, accession number to be added upon manuscript acceptance) from Ambohitsara-Tsitolaka. The 16S rDNA sequence of this specimen was 99% identical to a reference sequence of a *B. albipunctatus* adult specimen (accession AY848446) from Manantantely. One other voucher tadpole of *B. albipunctatus* from the same locality is morphologically very similar to the described voucher specimen.

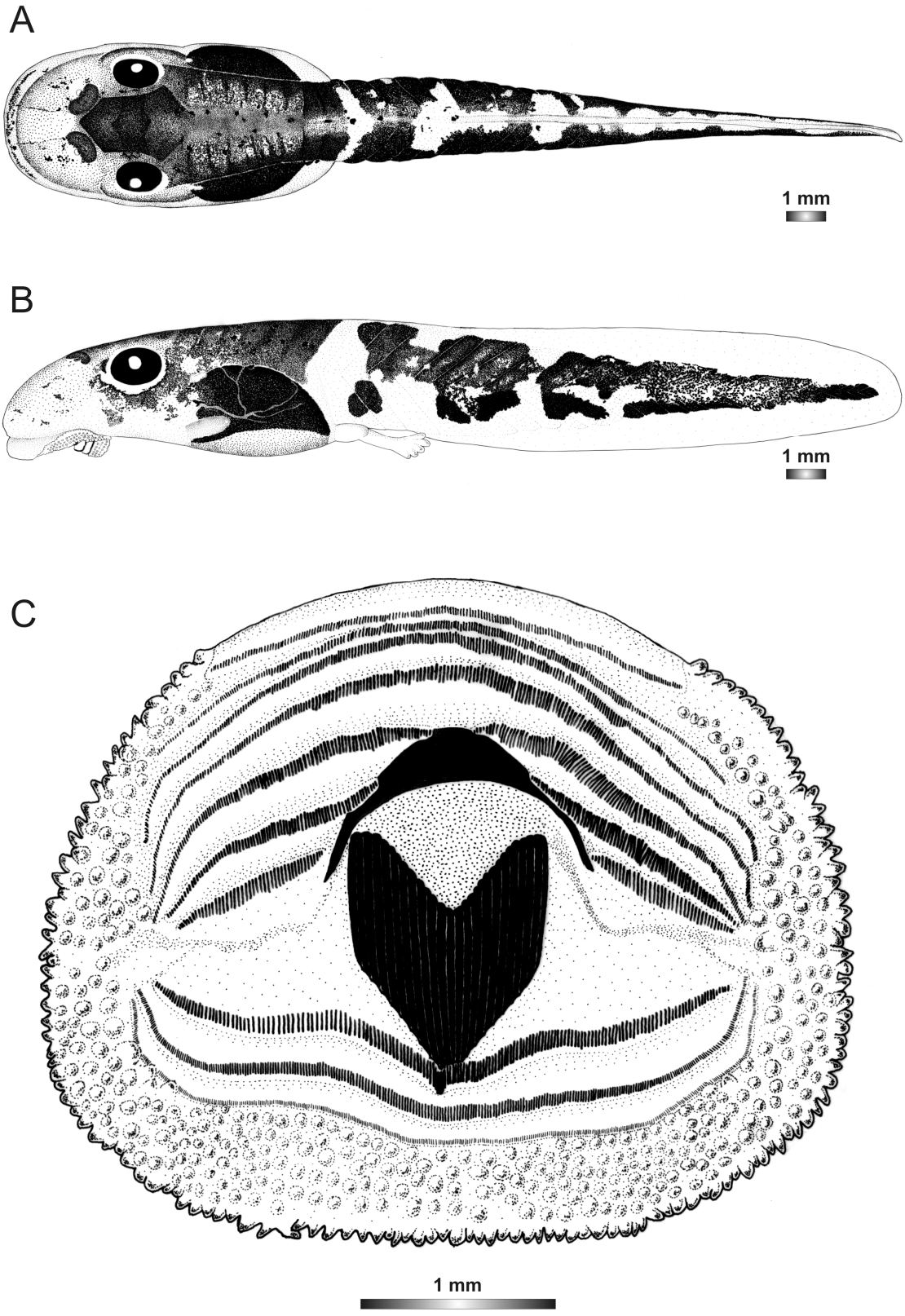

Figure 10. Drawings of the preserved DNA voucher tadpole of *Boophis luciae* (ZCMV 5146 - ZSM 730/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

B. albipunctatus tadpoles can be separated with those of *B. ankaratra* and *B. schuboeae* by the absence of the lateral bulge on the oral disk, the absence of the medial convexity on the upper sheath, the high number of papillae, and the lack of one interrupted tooth row on the upper labium which gives a LTRF 7(5-7)/3, but they share the ribbed pattern, the U-shaped, and the partially hidden state of the lower sheath. These tadpoles are also characterized by their less pigmented state in preservative which makes them easily to identify. The absence of silver tissue covering the heart in life is also typical for these tadpoles.

Boophis sibilans Glaw & Thiesmeier 1993

Morphological data were assessed in one tadpole (Figures 2 and 9) in developmental stage 29 (Field number FGZC 2956, ZSM 1631/2007, BL 11 mm, TL 26 mm, accession number to be added upon manuscript acceptance) from Marojejy National Park. The 16S rDNA sequence of this specimen was 99.4% identical to a reference sequence of *B. sibilans* adult specimen (accession AY341718) from Andasibe. Two other voucher tadpoles have the morphological characteristic of the species.

B. sibilans tadpoles have the same oral disk feature (absence of lateral bulge and the LTRF) as *B. albipunctatus*, except that they have a lower number of submarginal papillae and a V-shaped lower sheath. These tadpoles are characterized by their rather long tail (up to 200% of BL) and their unique tail pattern which is composed of dark spots separated by clear unpigmented area. The inner part of the spots is usually free from pigment.

Boophis luciae Glaw, Köhler, de la Riva, Vieites & Vences 2010

Morphological data were assessed in one tadpole (Figures 2 and 10) in developmental stage 36 (Field number ZCMV 5146, ZSM 730/2007, BL 10.4 mm, TL 22.2 mm, accession number to be added upon manuscript acceptance) from Ranomafana National Park. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of a *B. luciae* adult specimen (accession AY848444) from the same locality. Ten other voucher tadpoles are morphologically very similar to the described voucher specimen.

The tadpoles of *B. luciae* are similar to those of *B. sibilans* by the oral disk structure and the general external pattern except that they have a rather short tail. They can be characterized by the state of the spots on the tail musculature which are connected together.

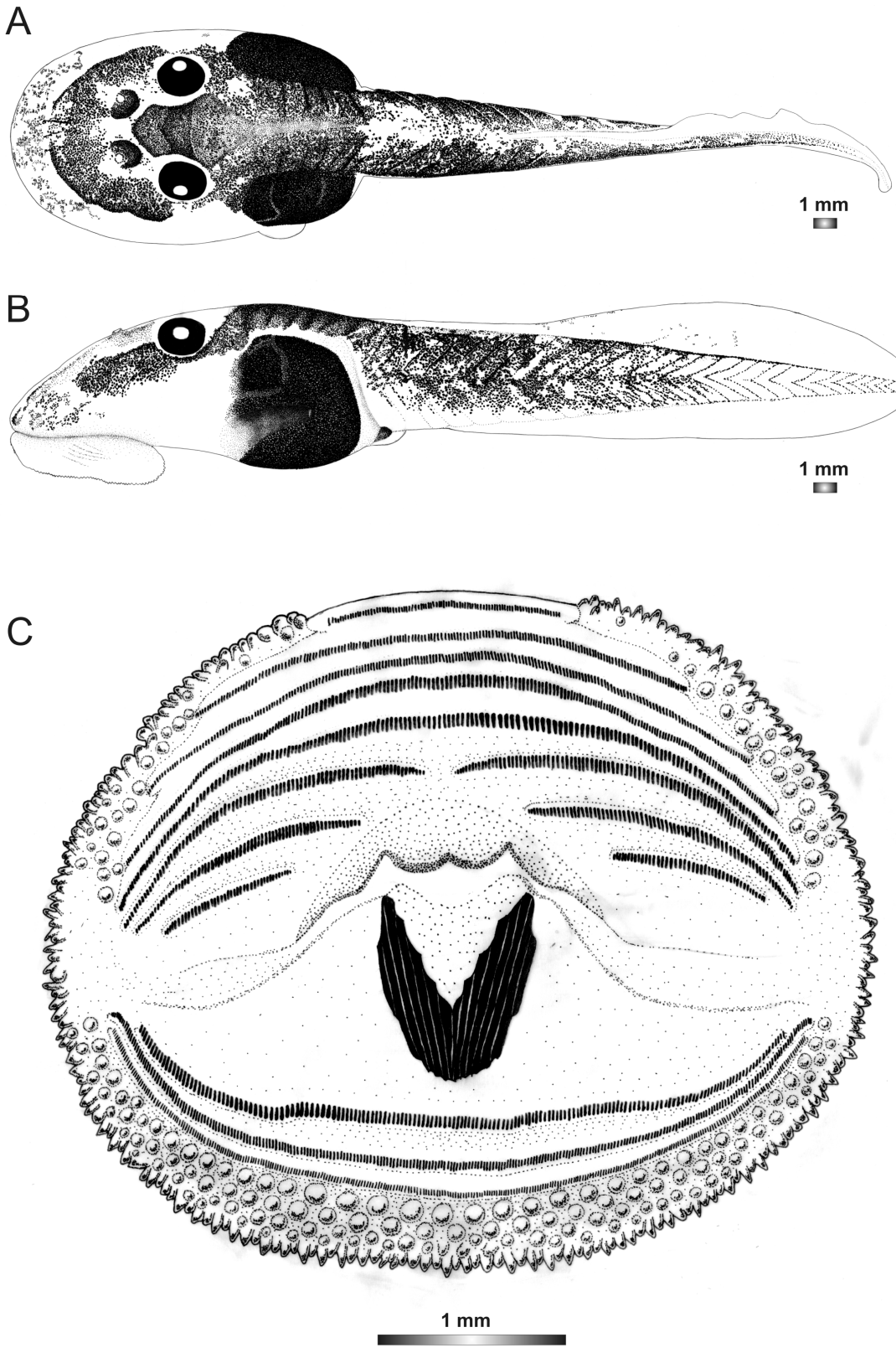

Figure 11. Drawings of the preserved DNA voucher tadpole of *Boophis sambirano* (FG/MV 2003-1904 - ZSM 678/2004): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

Boophis mandraka group

This group is characterized by tadpoles having an enlarged oral disk without lateral emargination and ventral gap of papillae. The dorsal gap of papillae is very narrow to narrow and the lateral area where the oral disk folds is free of submarginal papillae. The anterior margin of the oral disk is separated by a deep crevice to the snout; *i.e.*, the entire margin is free from the snout. The upper labium has always five uninterrupted and three interrupted tooth rows, and the three lower rows are always uninterrupted giving a unique LTRF 8(6-8)/3. The upper sheath is always absent. The lower sheaths are moderately strong and completely keratinized, U-shaped ribbed, and higher than wide. The dorsolateral glands are present.

B. sambirano Vences & Glaw 2005

Morphological data were assessed in one tadpole (Figures 2 and 11) in developmental stage 25 (Field number FG/MV 2002.1902, ZSM 672/2004, BL 6.5 mm, TL 12.7 mm, accession number to be added upon manuscript acceptance) from the Camp Norbert in Manongarivo Special Reserve. The 16S rDNA sequence of this specimen was 96% identical to a reference sequence of *B. sambirano* adult specimen (accession AY848544), and its identity belonging to the "true" *B. sambirano* therefore lacks further confirmation. Because it was collected next to the type locality of *B. sambirano*. Following a parsimonious approach we here assign this tadpole to this species, although the large numbers of distinct lineages in *B. sambirano* make it likely that yet another candidate species of this complex occurs in Manongarivo. Many non-voucher specimens of the same series present morphological similarities to the voucher specimen.

B. sambirano tadpoles are easily to distinguish with any other previous described tadpoles by the state of their oral disk which has no upper sheath, a short A_1 and a narrow dorsal gap of the papillae. The absence of submarginal papillae on the lateral area where the oral disk folds is shared with *B. schuboeae*. The tadpoles of this species are also characterized by the extension of the obvious lateral transparent area only on the 2/3 proximal of the body, but not surrounding the whole body like the other tadpoles.

Boophis mandraka [Ca38 Vieites et al. 2009]

Morphological data were assessed in one tadpole (Figures 2 and 12) in developmental stage 26 (Field number ZCMV 4261, ZSM 456/2007, BL 7.6 mm, TL 15.8 mm, accession number to be added upon manuscript acceptance) from Ranomafana National Park. The 16S

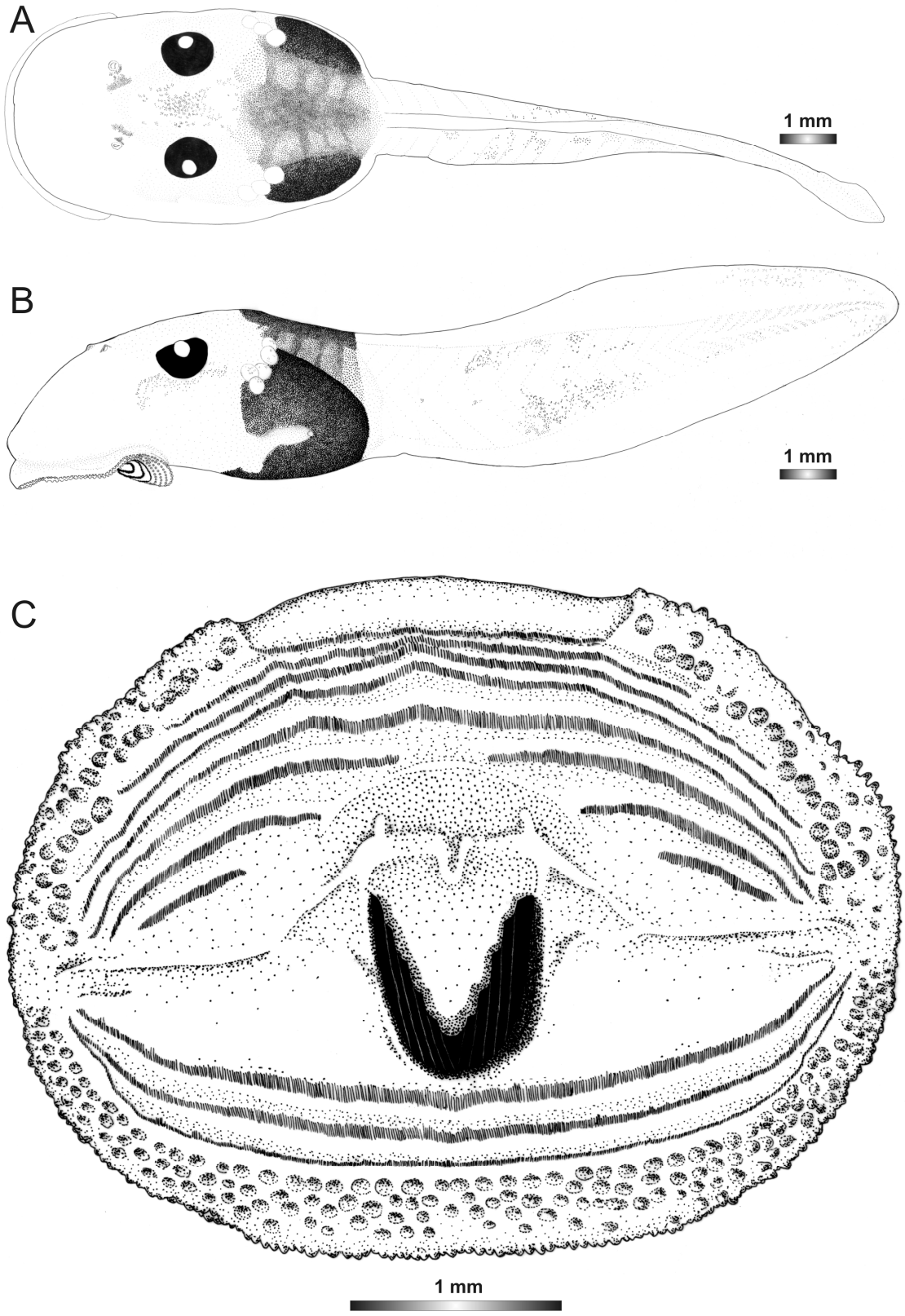

Figure 12. Drawings of the preserved DNA voucher tadpole of *B. mandraka* [Ca38] (ZCMV 4251 - ZSM 456/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

rDNA sequence of this specimen was 93.3% identical to a reference sequence of a *Boophis sambirano* adult specimen (accession EU717863) from Manongarivo Special Reserve.

The single tadpole of this candidate species has the similar structure of oral disk as those of *B. sambirano* except that it has a rather wide dorsal gap of papillae (DG/ODW 39% *vs.* 34%). The typical coloration, yellowish in life and whitish in conservative (losing almost all melanophoric pigment) and the well visibility of the 10 (5 right and 5 left) dorsolateral glands make it easily to distinguish from other tadpoles.

Boophis mandraka [Ca46 ZCMV 3479]

Morphological data were assessed in one tadpole (Figures 2 and 13) in developmental stage 25 (Field number ZCMV 3479, ZSM 1784/2007, BL 6.8 mm, TL 14.3 mm, accession number to be added upon manuscript acceptance) from An'Ala. The 16S rDNA sequence of this specimen was 90.4 % identical to a reference sequence of *Boophis* sp. aff. *mandraka* adult specimen (accession AY848542) from Ilampy.

The oral disk of the single tadpole of this candidate species is similar to those of *B. sambirano* and *B. mandraka* [Ca38] except that it has the narrowest dorsal gap of papillae with DG 14% of ODW and the shortest A_1 with 21% of ODW. Within the *Boophis mandraka* group tadpoles, it has also the lowest number of papillae. The external morphology of the single tadpole of this candidate species looks like those of *B. sambirano*, except that the ration RN/NP is much higher (194 *vs.* 125) and the pigmentation pattern is slightly different.

Boophis sambirano [Ca47 ZCMV 13105]

Morphological data were assessed in one tadpole (Figures 2 and 14) in developmental stage 27 (Field number ZCMV 13105, ZSM 482/2010, BL 13.5 mm, TL 27.1 mm, accession number to be added upon manuscript acceptance) from Anjingo river (bridge 57 km from Antsohihy to Bealanana). The 16S rDNA sequence of this specimen was 97% identical to a reference sequence of *Boophis sambirano* tadpoles (accession EU717861) from Manongarivo Special Reserve. Two other voucher tadpoles are morphologically very similar to the described voucher specimen.

The tadpoles assigned to this candidate species have a similar oral disk structure as *B. sambirano* exept that they have a higher number of marginal papillae (377 *vs.* 248) and of keratodont on A_3 (1193 *vs.* 740). These tadpoles have a rather big size in comparison with those of *B. mandraka* group, and their pigmentation pattern distinguishes them also. Their tail muscula-

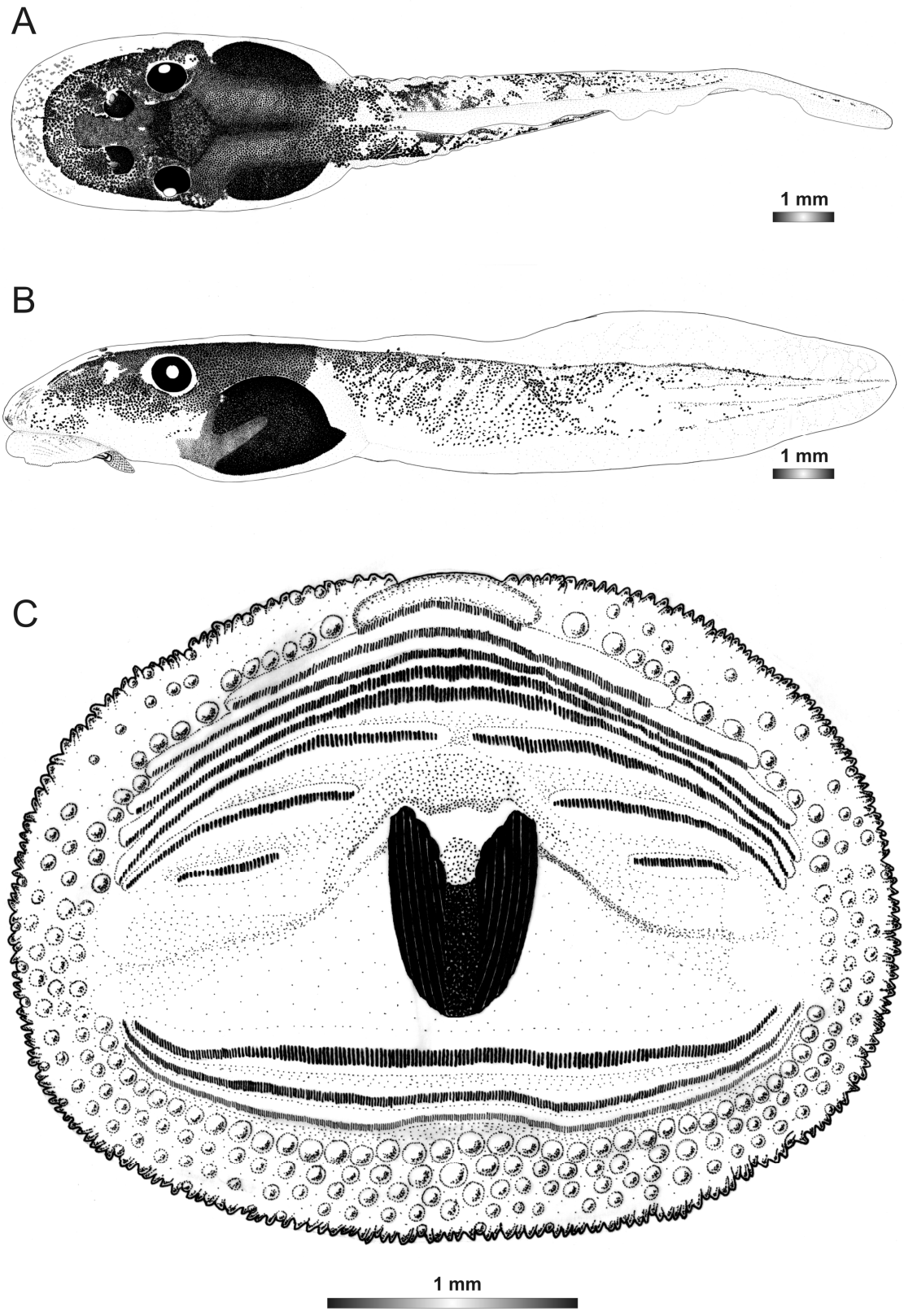

Figure 13. Drawings of the preserved DNA voucher tadpole of *B. mandraka* [Ca46] (ZCMV 3479 - ZSM 1784/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

ture is covered by dissipated remarkable patches following mainly the lateral tail vein and the myosepta on the half proximal of the tail musculature, and irregularly dispersed on the half distal, although it is just covered by dense spots on the proximal half in *B. sambirano* tadpoles. The dorsal fin of these tadpoles begins usually on the 1/5 proximal of the tail musculature, against surrounding the dorsal body-tail junction in *B. sambirano* tadpoles.

Boophis sambirano [Ca48 ZCMV 13109]

Morphological data were assessed in one tadpole (Figures 2 and 15) in developmental stage 27 (Field number ZCMV 13109, ZSM 485/2010, BL 12.7 mm, TL 24.7 mm, accession number to be added upon manuscript acceptance) from Anjingo river (bridge 57 km from Antsohihy to Bealanana). The 16S rDNA sequence of this specimen was 94% identical to a reference sequence of *Boophis sambirano* tadpoles (accession EU717861) from Manongarivo Special Reserve. Two other voucher tadpoles are very similar to the described voucher specimen.

The tadpoles assigned to this candidate species have a similar oral disk as *B. sambirano* and *B. sambirano* [Ca47]. The higher number of marginal papillae (336) and of keratodont on A_3 (1052) differentiate these tadpoles from those of *B. sambirano* but similar to those of *B. sambirano* [Ca47]. The ovoidal body form in dorsal view and the pigmentation pattern – variegated spots on the body and less coalesced spots on the tail musculature – differentiate these tadpoles from those of *B. sambirano* [Ca47]. The beginning of the dorsal fin on the 1/5 proximal of the tail musculature is similar to that of *B. sambirano* [Ca47] but different from *B. sambirano*.

Boophis sambirano [Ca49 ZCMV 13155]

Morphological data were assessed in one tadpole (Figures 2 and 16) in developmental stage 27 (Field number ZCMV 13155, ZSM 528/2010, BL 11.7 mm, TL 26.7 mm, accession number to be added upon manuscript acceptance) from Ankijagna Lagnana. The 16S rDNA sequence of this specimen was 94.1% identical to a reference sequence of *Boophis sambirano* tadpoles (accession EU717861) from Manongarivo Special Reserve. Three other voucher and many non-voucher specimens of the same series are morphologically very similar to the described voucher specimen.

The oral disk of the tadpoles assigned to this candidate species is the typical *B. mandraka* group tadpole oral disk characterized by the narrow dorsal gap (DG 23% of ODW) which is here bigger than those of *B. mandraka* [Ca46] but smaller than those of the other tadpoles, and the short A_1 which is almost the same as of *B. mandraka* [Ca46] tadpoles. The number of papillae is close to those of *B. sambirano* and *Boophis mandraka* [Ca38]. These tadpoles

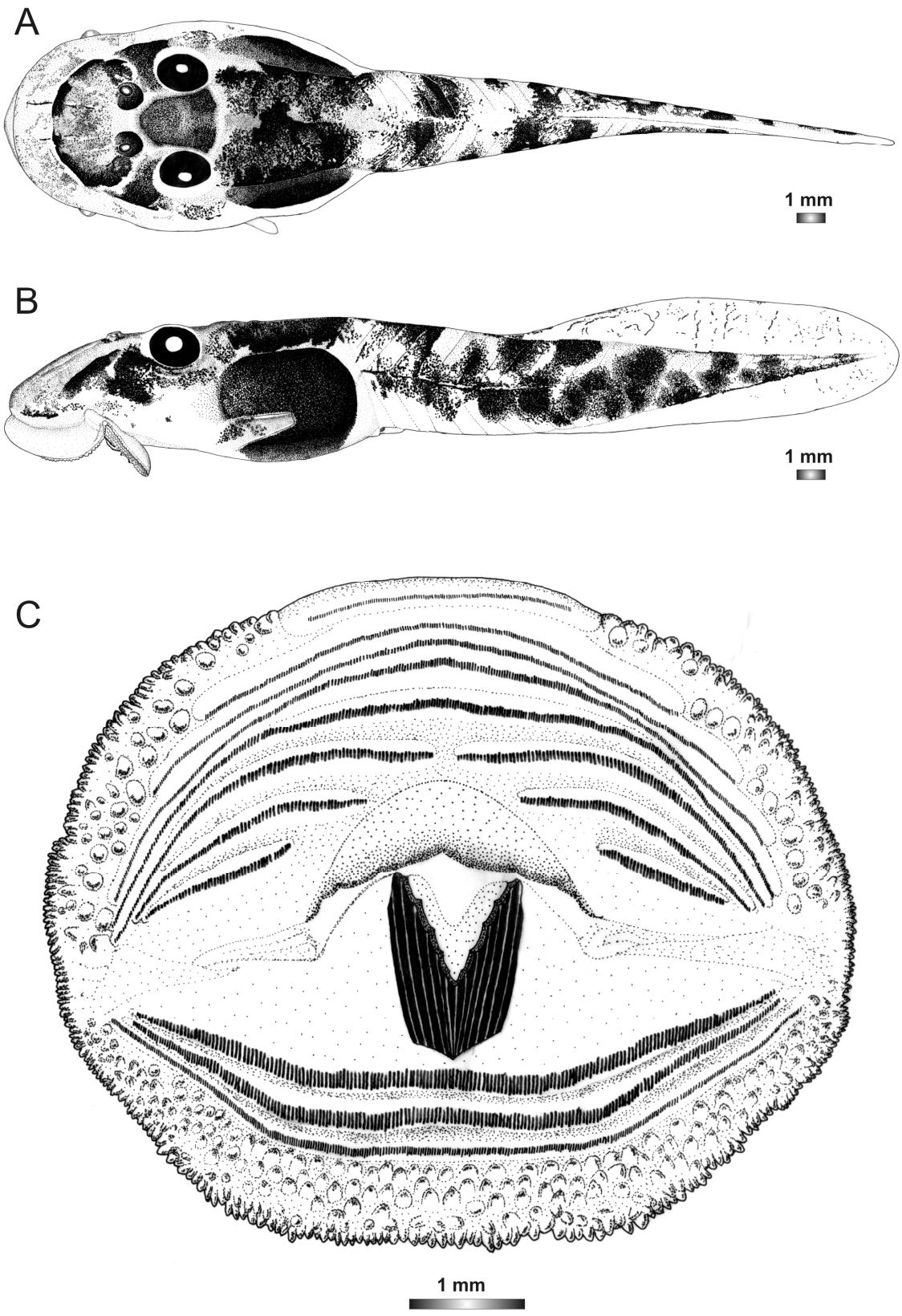

Figure 14. Drawings of the preserved DNA voucher tadpole of *B. sambirano* [Ca47] (ZCMV 13105 - ZSM 482/2010): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

can be easily distinguished from all *B. sambirano*-like tadpoles by their particular pigmentation pattern which is uniformly dark, the non visibility of the lateral transparent area surrounding the body, the ovoidal form of the body in dorsal view, and the eye situation between the 3/10 and 4/10 proximal of the body.

Boophis sambirano [Ca50 ZCMV 13172]

Morphological data were assessed in one tadpole (Figures 2 and 17) in developmental stage 27 (Field number ZCMV 13172, ZSM 545/2010, BL 11.7 mm, TL 25.7 mm, accession number to be added upon manuscript acceptance) from Ambinanitelo. The 16S rDNA sequence of this specimen was 94.9% identical to a reference sequence of *Boophis sambirano* tadpoles (accession EU717861) from Manongarivo Special Reserve. Three other voucher tadpoles are morphologically very similar to the described voucher specimen.

The oral disk of the tadpoles of this candidate species is identical to those of the species belonging to the same group. The tadpoles belonging to this candidate species have an elliptical body form in dorsal view but differentiate with those of *B. sambirano* [Ca49] by the pigmentation pattern. The presence of the lateral transparent area surrounding the proximal 2/3 of the body is similar to those of *B. sambirano*, but the pigmentation pattern distinguishes them. These tadpoles are characterized by the absence of contrast integumental patches limiting the transparent area surrounding the snout like in *B. sambirano*, *Boophis sambirano* [Ca47], and *Boophis sambirano* [Ca48]. The tadpoles of this candidate species are easy to distinguish from those of other candidate species close to *B. sambirano* by their coloration pattern.

Boophis majori group

This group is characterized by different types of tadpoles, but the tadpoles having an enlarged oral disk are without lateral emargination, dorsal and ventral gap of papillae. The submarginal papillae are complete. The anterior margin of the oral disk is separated by a deep crevice to the snout; *i.e.*, the entire margin is free from the snout. The upper labium has always four uninterrupted and three interrupted tooth rows, and the three lower rows are always uninterrupted giving a unique LTRF 7(6-7)/3. The jaw sheaths are moderately strong and completely keratinized. The upper sheath has always no medial convexity. The lower sheath is U-shaped, ribbed, and higher than wide. The dorsolateral glands are present.

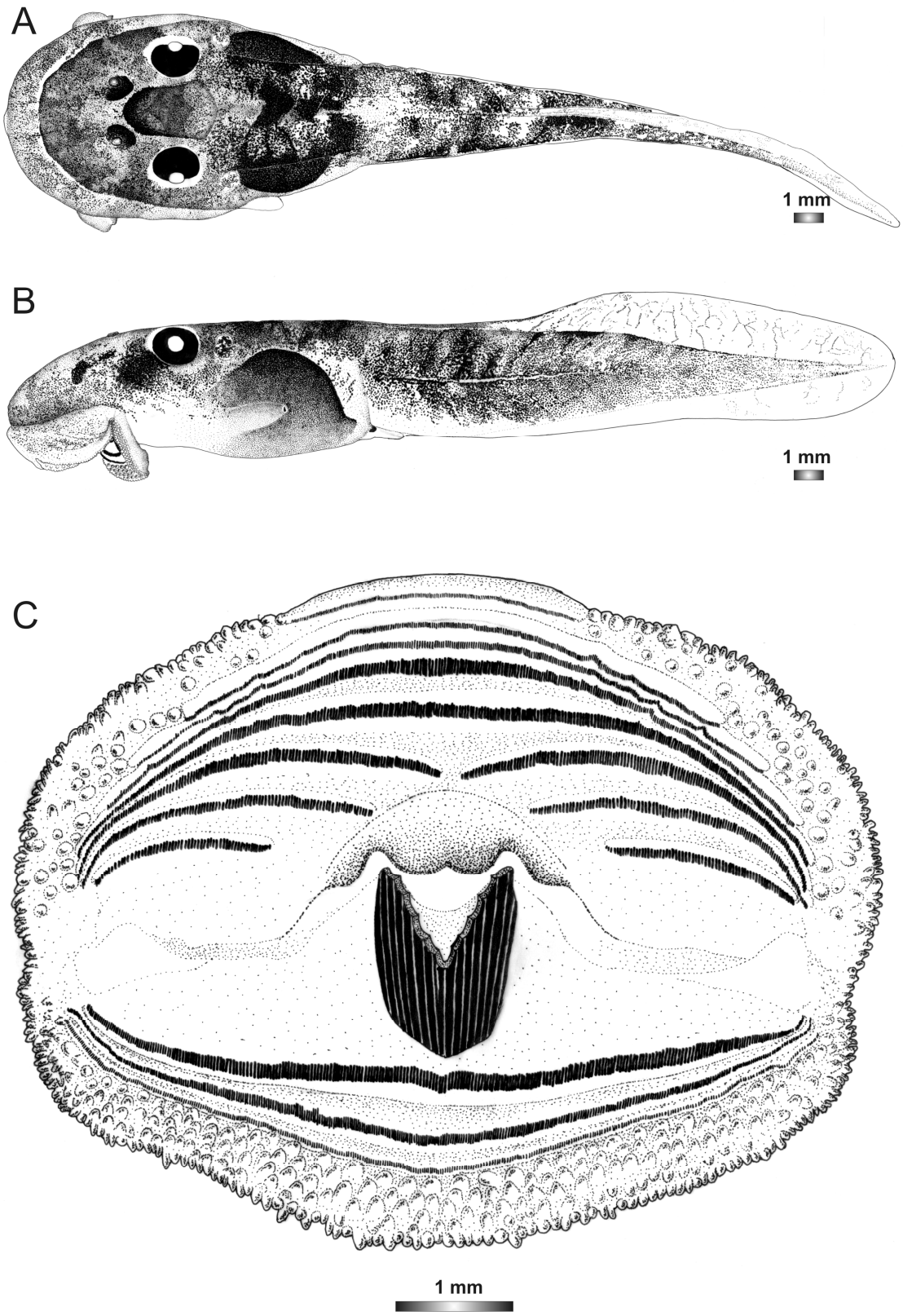

Figure 15. Drawings of the preserved DNA voucher tadpole of *B. sambirano* [Ca48] (ZCMV 13109 - ZSM 485/2010): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

Boophis marojezensis Glaw & Vences 1994

Morphological data were assessed in one tadpole (Figures 2 and 18) in developmental stage 27 (Field number FGZC 2277, ZSM 1528/2007, BL 7.1 mm, TL 18.3 mm, accession number to be added upon manuscript acceptance) from Marojejy National Park. The 16S rDNA sequence of this specimen was 99.8% identical to a reference sequence of *B. marojezensis* adult specimen (accession FJ559127) from the same locality. Three other voucher tadpoles are morphologically very similar to the described voucher specimen.

The tadpoles of this species are easily to distinguish with those belonging to other group by the general structure of their oral disk which has no dorsal gap of papillae, and the LTRF 7(6-7)/3. These tadpoles are also characterized by the highest number of papillae with 290 marginal and 606 submarginal papillae. The lateral transparent area is visible and the dorsolateral gland is obvious. The tail muscle is spotted and the spots fused to form patches mainly on the upper half of tail musculature, the density of the spots diminished toward the tail tip. The 1/3 distal of the tail has few pigments.

Boophis marojezensis [Ca25 Vieites et al. 2009]

Morphological data were assessed in one tadpole (Figures 2 and 19) in developmental stage 29 (Field number FGZC 2929, ZSM 1611/2007, BL 7.8 mm, TL 18.5 mm, accession number to be added upon manuscript acceptance) from Marojejy National Park. The 16S rDNA sequence of this specimen was 97% identical to a reference sequence of *B. marojezensis* adult specimen (accession AY848596) from Vohidrazana. Two non voucher specimens from the same series present the particular caudal pattern presented in the voucher specimen.

Tadpoles assigned to this candidate species has the same oral disk structure as those of *B. marojezensis*, but with less number of papillae (222 marginal and 315 submarginal). The presence of seven more or less rounded patches formed by condensation of spots on the half distal of the tail musculature of these tadpoles is useful to differentiate them from those of *B. marojezensis*.

Boophis marojezensis [Ca26 Vieites et al. 2009]

Morphological data were assessed in one tadpole (Figures 2 and 20) in developmental stage 29 (Field number FGZC 2930, ZSM 1612/2007, BL 8.8 mm, TL 20.6 mm, accession number to be added upon manuscript acceptance) from Marojejy National Park. The 16S rDNA sequence of this specimen was 96.6% identical to a reference sequence of *B. marojezensis* adult specimen (accession AY848595) from Tsaratanana.

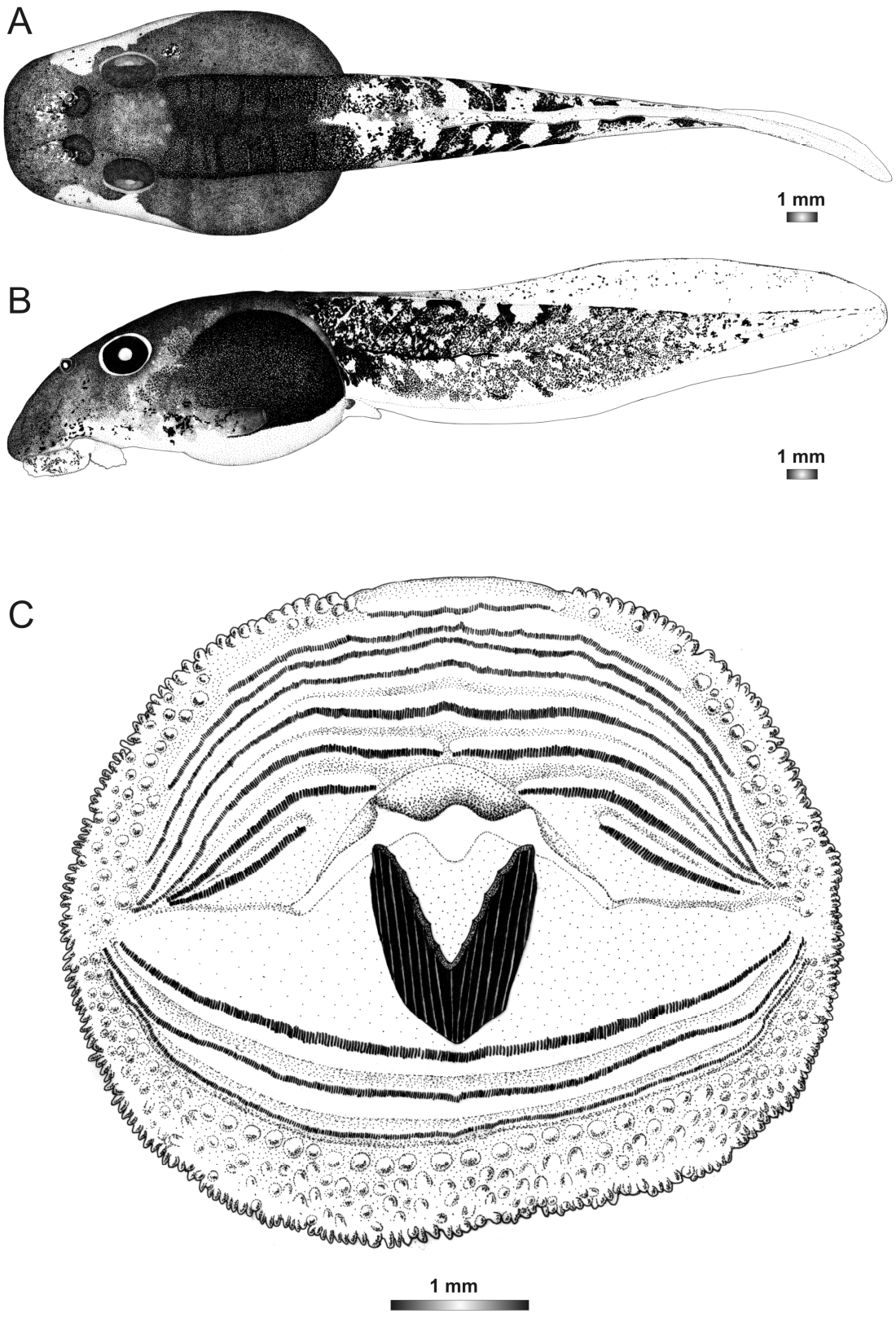

Figure 16. Drawings of the preserved DNA voucher tadpole of *B. sambirano* [Ca49] (ZCMV 13155, ZSM 528/2010): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

The single tadpole belonging to this candidate species has the typical *marojezensis*-like oral disk structure with 234 marginal and 430 submarginal papillae. It has almost the same pigmentation pattern as *B. marojezensis*, but the patches are more striking on the upper limit of tail musculature. It differentiates with *B. marojezensis* [Ca25] by the absence of distinct patches on the tail musculature.

Boophis marojezensis [Ca51 ZCMV 3691]

Morphological data were assessed in one tadpole (Figures 2 and 21) in developmental stage 25 (Field number ZCMV 3691, ZSM 267/2008, BL 6 mm, TL 20 mm, accession number to be added upon manuscript acceptance) from Ranomafana National Park. The 16S rDNA sequence of this specimen was 99.7% identical to a reference sequence of a *B. marojezensis* adult specimen (accession AY848594) from Vohiparara. Twenty one other tadpoles assigned to this candidate species reveal similar morphological pattern and oral disk configuration as the described voucher specimen.

The oral disk of the tadpoles assigned to this candidate species is a typical *marojezensis*-like with 297 marginal and 309 submarginal papillae. It can be distinguished with the other *marojezensis*-like tadpoles by the absence of the lateral transparent area surrounding the body and they have also the widest inter-orbital distance (IOD) and they are also the only *marojezensis*-like tadpoles which have eyes situated between the 3/10 and 4/10 proximal of the body. The tail muscle is covered by reticulations, mainly on the half proximal.

Boophis marojezensis [Ca52 ZCMV 13168]

Morphological data were assessed in one tadpole (Figures 2 and 22) in developmental stage 28 (Field number ZCMV 13168, ZSM 541/2010, BL 10.5 mm, TL 26.1 mm, accession number to be added upon manuscript acceptance) from Ambinanitelo. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult specimen assigned to *B. marojezensis* (accession AY848595) from Tsaratanana (but with >5% divergence to all other *B. marojezensis*-like forms). One other voucher specimen is morphologically very similar to the described voucher specimen.

Tadpoles of this candidate species have the typical *marojezensis*-like oral disk structure with 258 marginal and 522 submarginal papillae. These tadpoles are characterized by the poorly visibility of the lateral transparent are surrounding the body and the tail pigmentation pattern, but the eyes situation is in the range with the other *B. marojezensis*-like tadpoles.

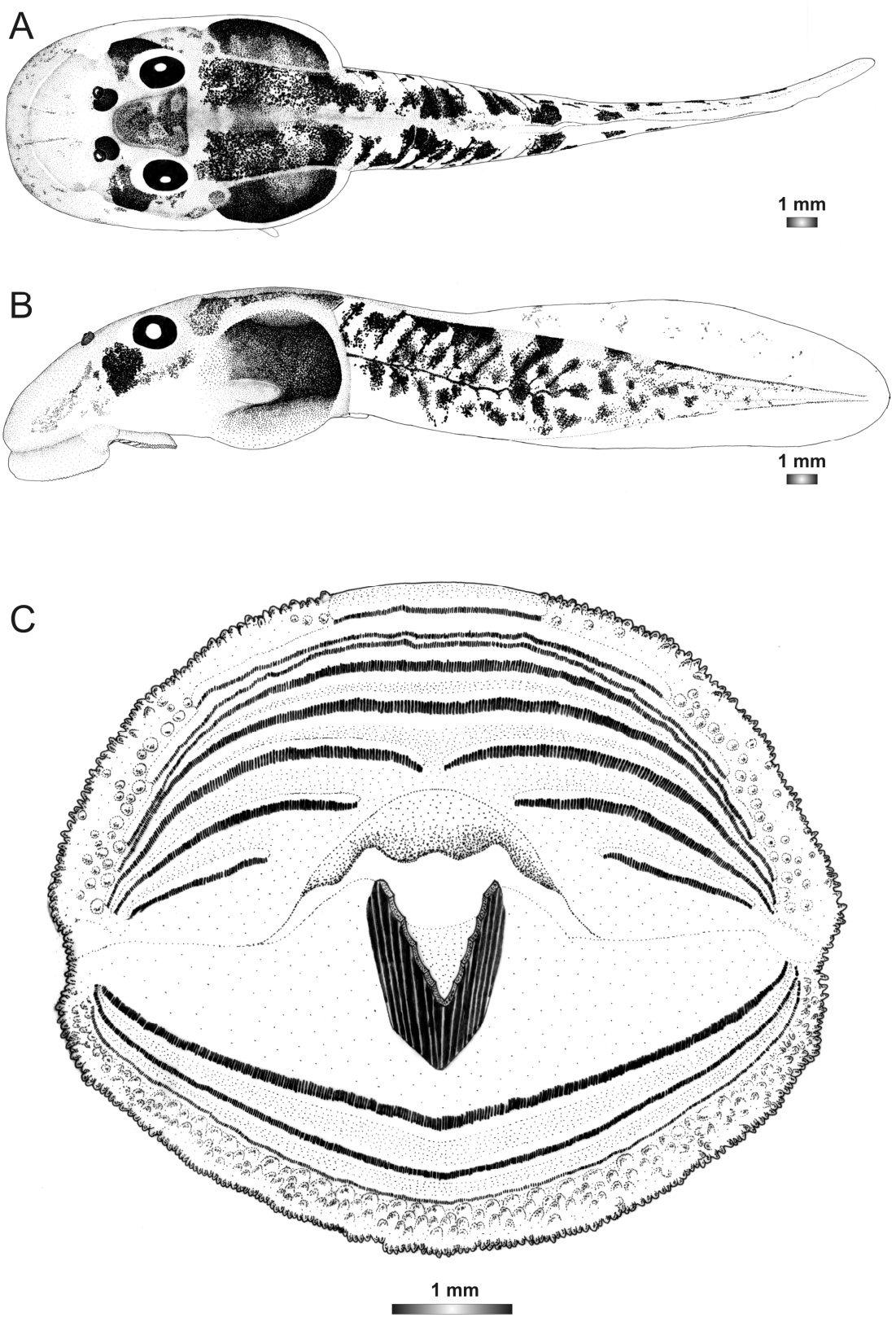

Figure 17. Drawings of the preserved DNA voucher tadpole of *B. sambirano* [Ca50] (ZCMV 13172 - ZSM 545/2010): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

Boophis marojezensis [Ca53 ZCMV 13200]

Morphological data were assessed in one tadpole (Figures 2 and 23) in developmental stage 27 (Field number ZCMV 13200, ZSM 573/2010, BL 9.6 mm, TL 23 mm, accession number to be added upon manuscript acceptance) from Tsaratanana Integral Reserve. The 16S rDNA sequence of this specimen was 98.8% identical to a reference sequence of a *B. marojezensis* adult specimen (accession FJ559127) from Marojejy. Five other voucher specimens attributed to the same candidate species are morphologically very similar to the described one.

The tadpoles of this candidate species have also a *marojezensis*-like oral disk with 243 marginal and 452 submarginal papillae. They are similar to *B. marojezensis*, *B. marojezensis* [Ca25] and *B. marojezensis* [Ca26], but distinct to *B. marojezensis* [Ca51] and *B. marojezensis* [Ca52] by the presence of the lateral clear area surrounding the body. The pigmentation pattern is similar to those of *B. marojezensis* [Ca26].

Boophis vittatus Glaw, Vences, Andreone & Vallan 2001

Morphological data were assessed in one tadpole (Figures 02 and 24) in developmental stage 29 (Field number FGZC 2238, ZSM 1906/2007, BL 7.8 mm, TL 18.5 mm, accession number to be added upon manuscript acceptance) from Marojejy National Park. The 16s rDNA sequence of this specimen was 100% identical to a reference sequence of a *B. vittatus* adult specimen (accession FJ559158) from the same locality. Three other voucher tadpoles of *B. vittatus* are morphologically very similar to the described voucher specimen.

The tadpoles of *B. vittatus* are the smallest tadpoles in this category. They have also a *marojezensis*-like oral disk structure with 289 marginal and 326 submarginal papillae. The tadpoles of this species are provided by a transparent lateral area which is more pronounced surrounding the 2/3 proximal of the body. The tail musculature is reticulated like in *B. marojezensis* [Ca51].

2. Ecological analysis

In Ranomafana National Park streams in the wet season, tadpoles of 44 frog species were found of which five belong to the group of strongly rheophilous *Boophis*. Those species were found in eleven out of 33 streams. Of those, *Boophis andohahela* occurred in eight streams with a mean of 9.9 specimens (min=1 to max=31 specimens), *B. ankaratra* occurred in two streams with each one single specimen, *Boophis marojezensis* [Ca51] was found in seven streams with a mean of 6.3 specimens (1 to 16 specimens), and only a single specimen of *B. schuboeae* was found. The tad-

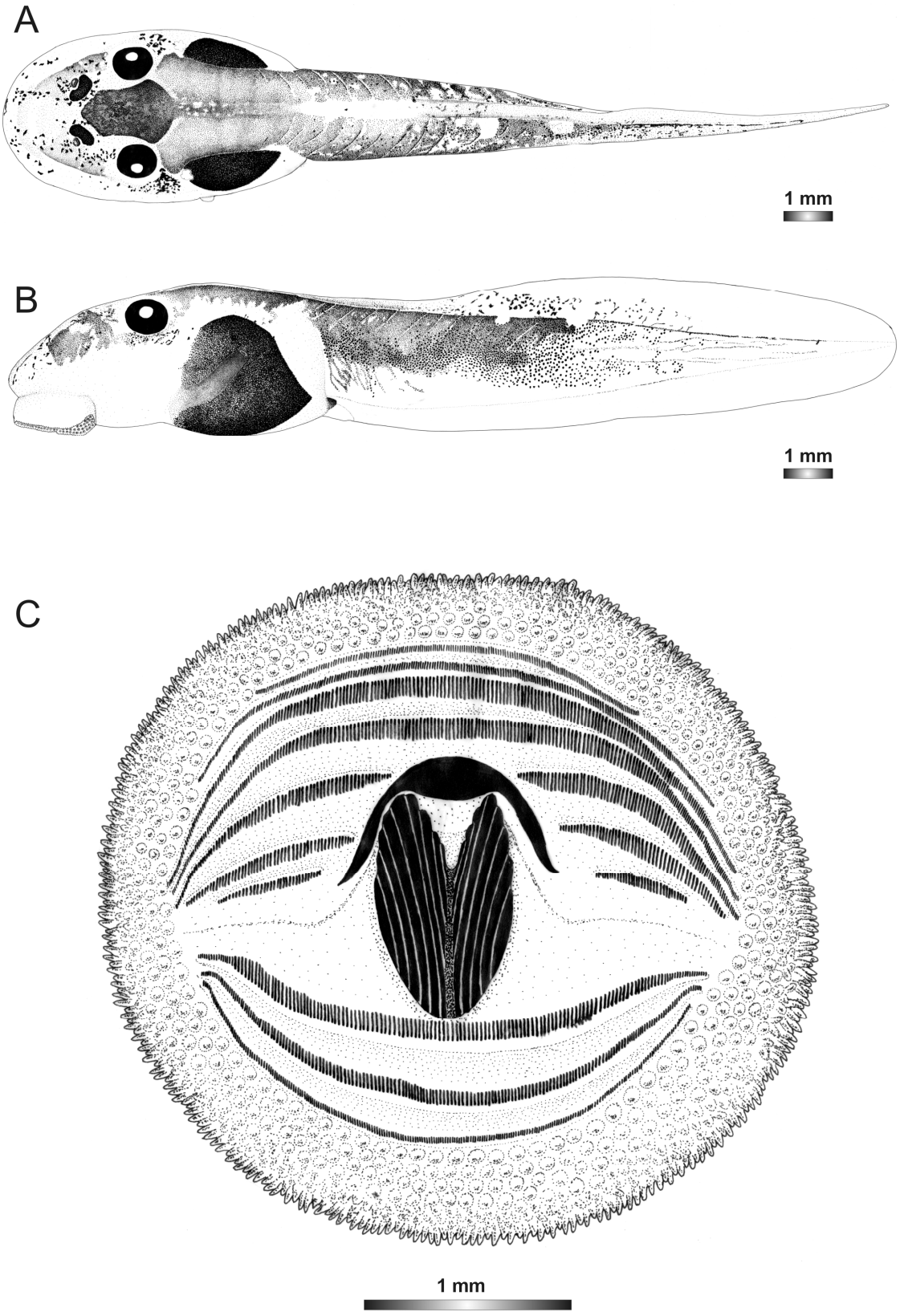

Figure 18. Drawings of the preserved DNA voucher tadpole of *B. marojezensis* (FGZC 2277 - ZSM 1528/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

poles of *B. luciae* (named *B.* sp. 17 in Vieites et al. 2009) were found in eight streams with a mean of 12 specimens (1 to 33). During a survey in Ranomafana National Park that was conducted in dry season, 23 species were found of which three belong to the group of strongly rheophilous *Boophis*. Those species were found in 30% of the sampled streams in this season. *B. andohahela* occurred in 23% of the streams with nine specimens on average, *Boophis marojezensis* [Ca51] occurred in 30% of the sampled streams with three specimens on average, and *B. luciae* occurred in 15% of the sampled streams with eight specimens on average.

3. Breeding site choice

Principal Component Analysis on the habitat variables of the stream and the surrounding forest resulted in three principal components, explaining together 65.5% of the variation in the data. We identified the following habitat variables being well represented (Figure 27): PC1 (33.8%) positive: slope and canopy cover of forest and stream, overhanging vegetation; negative: with and depth of the stream. Also four of the strongly rheophilous tadpole species, *B. ankaratra*, *B. andohahela*, *B. luciae*, and *B. marojezensis* [Ca51] are negatively correlated with this PC. The strongest contributors to PC2 (17.6%) were positive: forest leaf litter depth, stream overhanging plants, trees, and stream canopy cover; negative: slope of forest and stream. *B. andohahela* and *Boophis marojezensis* [Ca51] are negatively correlated with this PC. To PC3 (14.1%) were positive: number of small trees and shrubs in the forest and overhanging vegetation. Due to its rareness, no correlation of *B. schuboeae* incidence and PCs can be measured.

4. Microhabitat choice

Strongly rheophilous *Boophis* tadpoles have been found in all microhabitats available (Figure 28). Interestingly, a considerable amount of specimens was found in microhabitats characterised by fast flowing water and substrate of rock, gravel, and sand which generally harbour not many tadpoles (own unpublished data). Tadpoles of *B. andohahela* were also relatively often found in slow moving parts of the streams with leaves and sand as substrates. Of the two locally rare species, *B. ankaratra* and *B. schuboeae*, one specimen of each was found in fast rock and fast sand microhabitat, and one specimen in slow rock microhabitat, respectively.

Considering the availability of microhabitats in the streams, Ivlev's electivity index (E, Ivlev 1961) shows that strongly rheophilous *Boophis* do not show microhabitat preferences or avoidance except for "slow gravel" which is avoided by all species, and there is no general

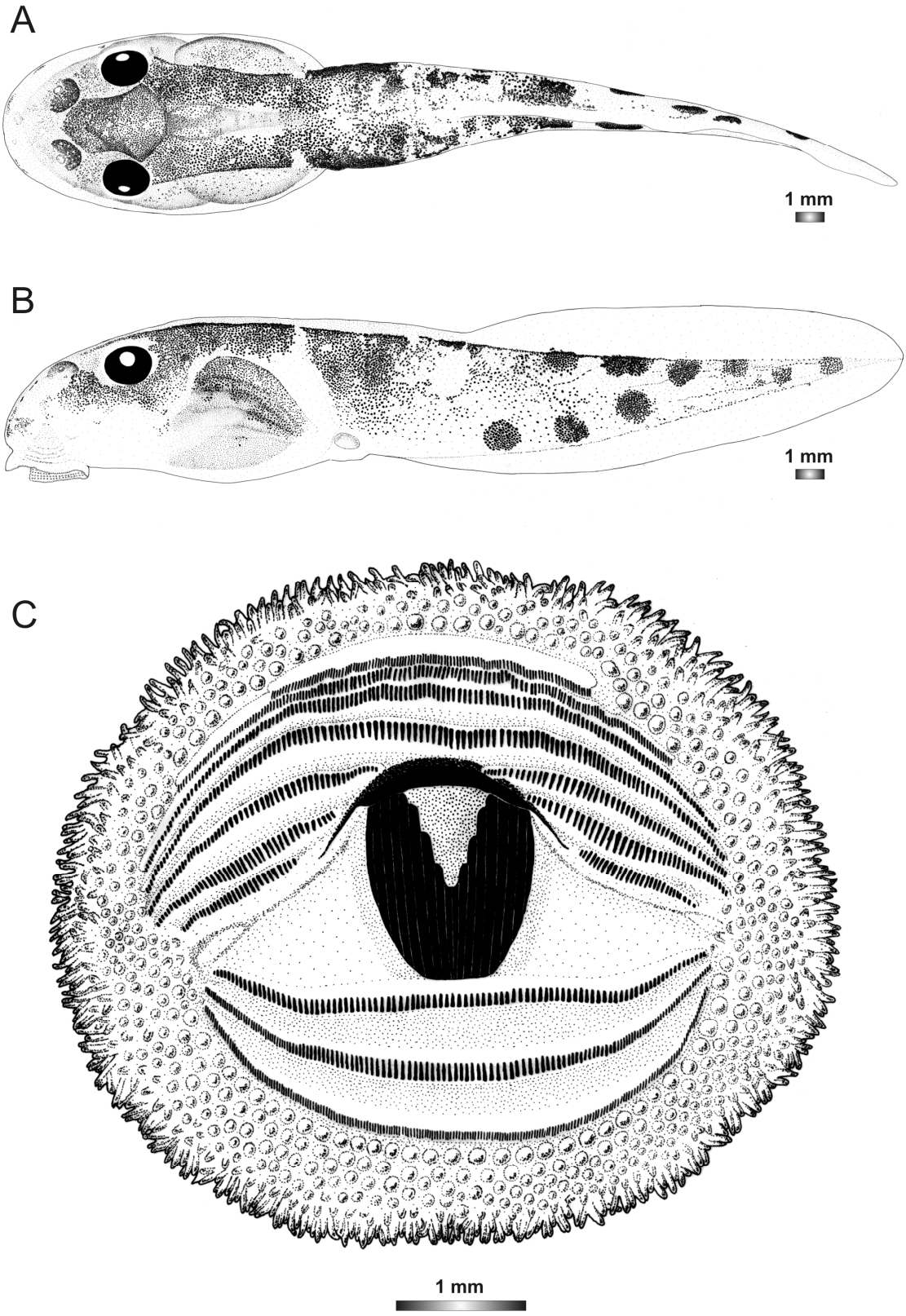

Figure 19. Drawings of the preserved DNA voucher tadpole of *B. marojezensis* [Ca25] (FGZC 2929 - ZSM 1611/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

difference between the three species (Figure 28; factorial ANOVA without interaction term including only streams with at least eight specimens of the respective species; $F_{9,53}$=1.716, p_{model}=0.108, p_{SG}=0.008, all other p including the factor "species" p>0.26). As interaction terms could not be included in this factorial ANOVA due to overparameterisation, we performed ANOVAs of subsets of the data and found that inter-species differences could only be shown for the microhabitat "fast rock" which is strongly avoided by *B. andohahela* (ANOVA of microhabitat subset; $F_{2,5}$=22.6, p_{model}=0.003, $p_{B.\ andohahela}$<0.001) whereas *B. marojezensis* [Ca51] and *B. luciae* were found much more often than *B. andohahela* ($p_{B.\ marojezensis\ [Ca51]}$=0.003, $p_{B.\ luciae}$=0.002). For "slow sand", only for *B. marojezensis* [Ca51] an avoidance could be detected (ANOVA of microhabitat subset; $F_{2,5}$=3.829, p_{model}=0.098, $p_{B.\ marojezensis\ [Ca51]}$=0.047), *B. andohahela* and *B. luciae* used "slow sand" as much as available ($p_{B.\ andohahela}$=0.427, $p_{B.\ luciae}$=0.105). For all other microhabitats, no significant difference in microhabitat use of species could be detected. However, it needs to be noticed that missing significances can be caused by the number of replicates (streams) which were reduced as we considered only streams with at least eight specimens of the respective species. A graphical evaluation of microhabitat use indicates that non-preference or non-avoidance is in fact present (Figure 29).

Discussion

1. Comparisons to previous descriptions of strongly rheophilous *Boophis* tadpoles

Twenty-two strongly rheophilous tadpoles are described in this study, including fourteen tadpoles that are described for the first time and eight other species that are previously described by other authors. Strongly rheophilous tadpoles are known for a long time by the works of Blommers-Schlösser (1979) in which *B. majori*, *Boophis* sp., *B. erythrodactylus*, and *B. mandraka* larvae were described.

The tadpoles of *B. majori* described by Blommers-Schlösser (1979) correspond to *B. marojezensis* according to the general external morphology with the sinistral spiracle situated on the 3/4 of the body, the well developed caudal musculature, the dark pattern on the body dorsum, the golden ventral side, the oral disk composed by complete small papillae, the lower jaw sheath that is higher than wide, the presence of an upper jaw sheath, and the LTRF of 7(5-7)/3. However, the finding of a dorsal gap of the papillae in some tadpoles is not in accordance with our description, because all *marojezensis*-like tadpoles (*B. marojezensis, B. marojezensis* [Ca25], *B.*

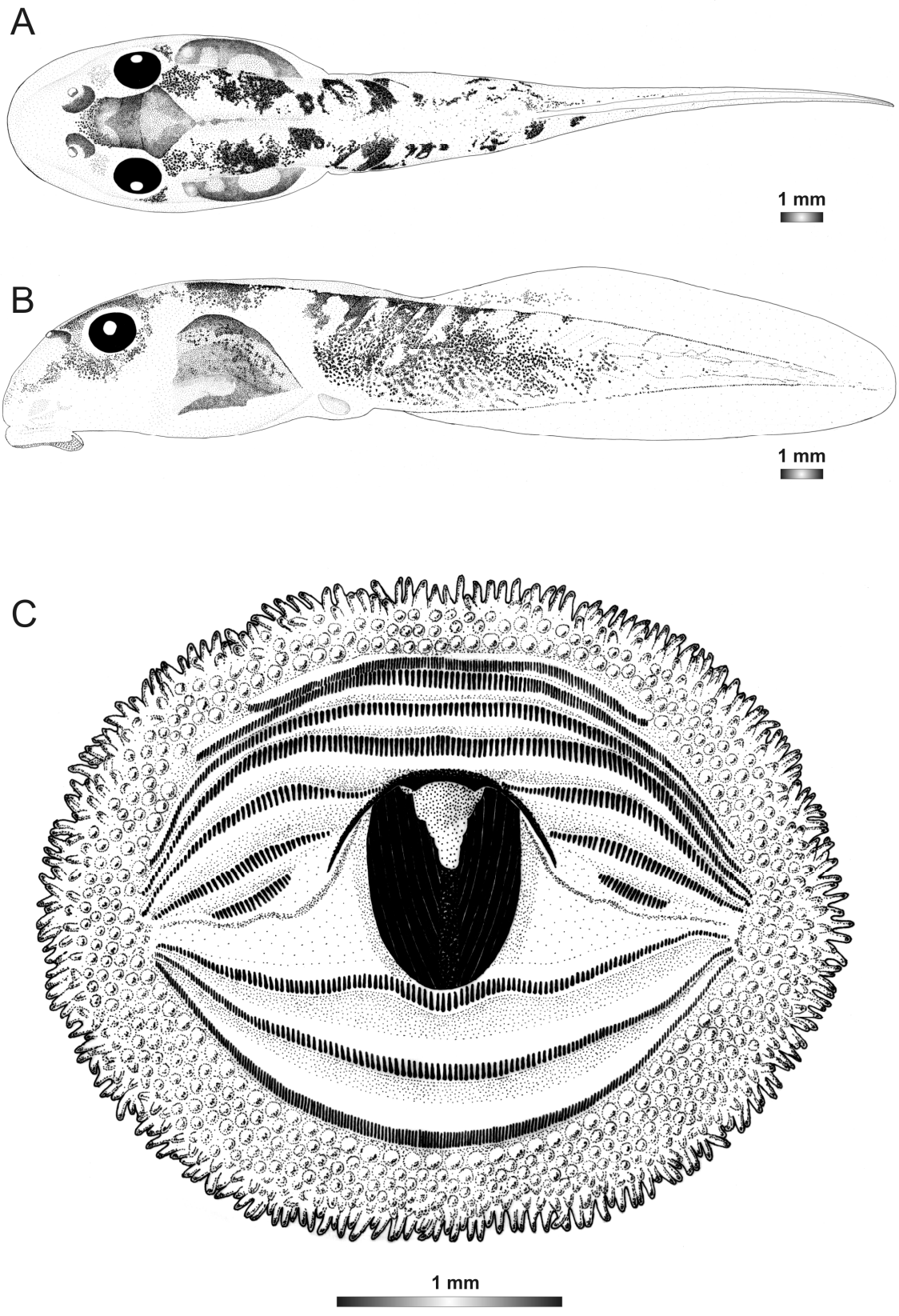

Figure 20. Drawings of the preserved DNA voucher tadpole of *B. marojezensis* [Ca26] (FGZC 2930 - ZSM 1612/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

marojezensis [Ca26], *B. marojezensis* [Ca51], *B. marojezensis* [Ca52], *B. marojezensis* [Ca53], and *B. vittatus*) that we describe have no dorsal gaps of papillae. We conclude therefore that those tadpoles might be strongly rheophilous tadpoles from other species of the *B. albipuctatus* group. Additionally, the relative tail length which is two times of the body length and the situation of the nares close to the eyes of the tadpoles examined by Blommers-Schlösser (1979) do not agree with our data, because all relevant tadpoles in this study have a rather short tail (TAL 166 - 188% of BL) and an opening of the nares that is closer to the snout than to the eyes or in the middle (RN/NP 78 – 103%). Later, Raharivololoniaina et al. (2006) described tadpoles of *B. marojezensis* from Andasibe which have the *marojezensis*-like morphology. The tadpoles of *Boophis* sp. (Blommers-Schlösser 1979) are similar to the *B. luteus* group tadpoles described herein according to their general oral disk structure shown in Figure 132 (page 308). The LTRF 6(3-6)/3(1) corresponds to those of *B. englaenderi* tadpoles and 6(3-6)/3 to those of *B. englaenderi* [Ca45] tadpoles indicates that those tadpoles might belong into two different *Boophis* species. As, none of the two corresponding species cited above distribute in the site where *Boophis* sp. tadpoles were found, those tadpoles must belong to species in *B. luteus* group whose larval stages are not yet known.

Tadpoles having narial openings closer to the eyes than to the snout, a sinistral spiracle situated on the 3/4 of the body, a well developed caudal musculature, a rounded oral disk with LTRF being 7(5-7)/3, a dorsal gap of papillae and a complete jaw sheath were also described and assigned to *Boophis erythrodactylus* by Blommers-Schlösser (1979). The species identification of those tadpoles, however, is uncertain (already mentioned by Raharivololoniaina et al. [2007]), because of the fact that *(1)* all the other species occurring in the *B. luteus* group have generalized tadpoles (see *B. rappiodes* in Blommers-Schlösser (1979) and Raharivololoniaina et al. (2006), *B. tasymena* and *B. viridis* in Raharivololoniaina et al. (2006), and *B. bottae* in Randrianiaina et al. [2009]); and *(2)* those tadpoles were stated being sympatric with *B. mandraka* tadpoles, and either might just be a variation of *B. mandraka* tadpoles or belong to a closely related species of *B. mandraka* (with similar tadpoles). As we encountered in our study, the tadpoles of two closely relative species can live sympatrically. But as we have not yet found the larval stage of this species, we can not fully reject the assumption of Blommers-Schlösser (1979) because a species group can be composed of different species with divergent larval morphologies (see *B. majori* group tadpoles in Schmidt et al. [2008] and Grosjean et al. [2011]).

As described by Blommers-Schlösser (1979), the tadpoles of *B. mandraka* have a sinistral spiracle that opens at 2/3 of the body, narial openings closer to the eyes than to the snout, a tail that is two times longer than the body, a well developed caudal musculature, a silvery belly, an almost rounded oral disk with a V-shaped lower sheath, and a LTRF 7(6-7)/3. In the *B. mandraka*

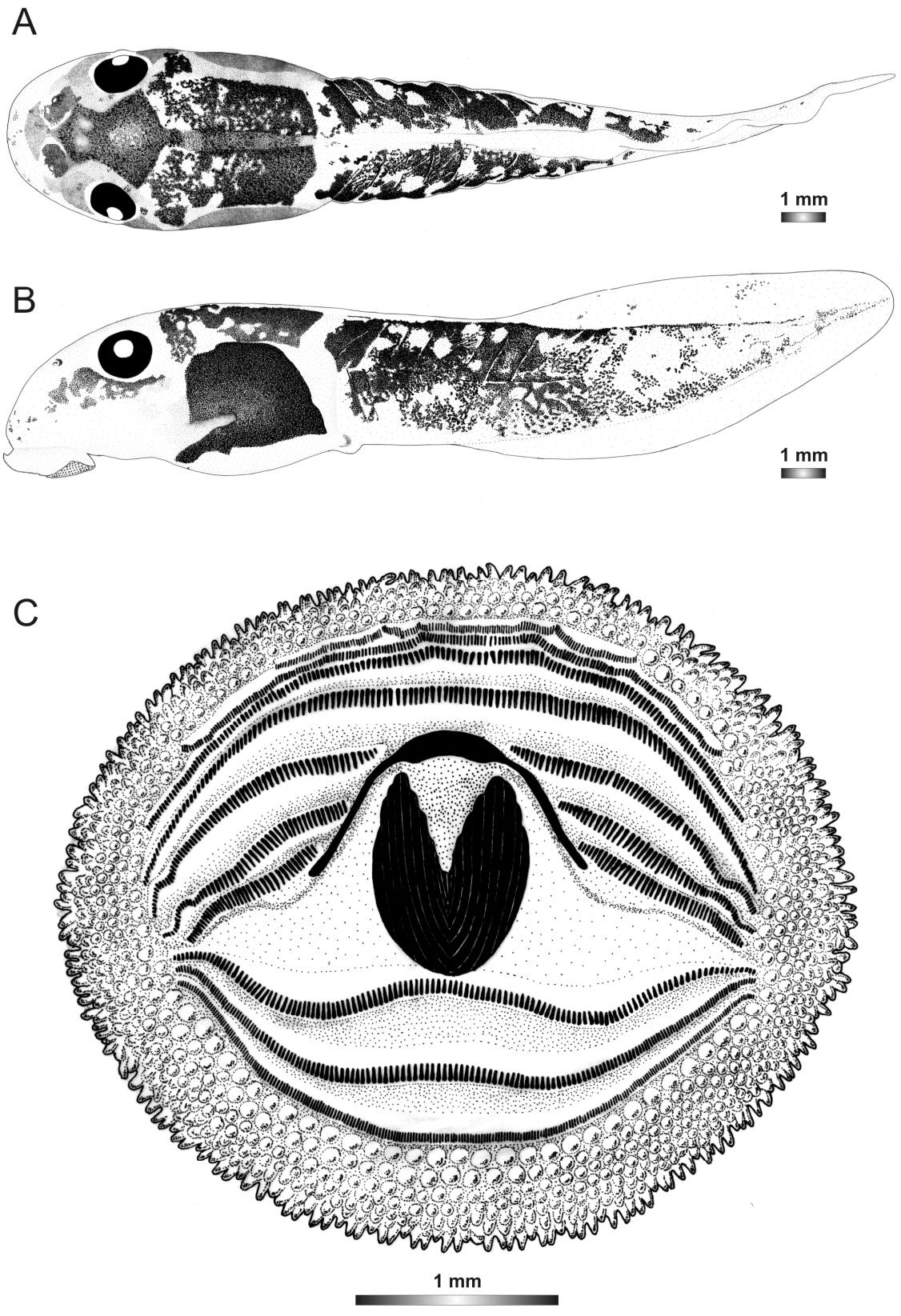

Figure 21. Drawings of the preserved DNA voucher tadpole of *B. marojezensis* [Ca51] (ZCMV 3691 - ZSM 267/2008): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

group, the tadpoles of *Boophis mandraka* are known to have an oral disk with complete papillae and a LTRF of 9(6-9)/3. So far no strongly rheophilous tadpoles with only two interrupted upper tooth rows have been observed in our study. We have observed in some tadpoles of *B. sibilans* and *B. luciae* that the gap separating the A_5 row is very tight which might be responsible for the false impression of an uninterrupted row. As the tadpoles in this study are closely related to *B. sambirano*, the affiliation of those tadpoles to *B. mandraka* can be confirmed.

Tadpoles of *B. andohahela* from Ranomafana were described by Thomas et al. (2006). The general morphology and the oral disk structure of the tadpoles agree with our specimens, except the tooth row formula and the presence of a ventral gap of marginal papillae. Thomas et al. (2006) described tadpoles with a LTRF 6(3-6)/3(1), although in our study all tadpoles from the same locality as in Thomas et al. (2006) have a LTRF 6(3-6)/3. This might be caused by the fact that the teeth in the first lower row are very dense, and sometimes it folds in the middle giving the mistaking impression of a gap.

The *B. sibilans* tadpoles from Andasibe that Raharivololoniaina et al. (2006) described agree with our specimen except some minor differences; *e.g.*, the relative width of the oral disk. These differences might be due to the different developmental stages of the tadpoles in the two studies, or by the different methods that have been used.

Glos et al. (2007) described the tadpoles of *B. schuboeae* from Ranomafana and *B. ankaratra* from Andringitra. The morphology therein is in accordance to the specimens of our study.

B. englaenderi, *B. vittatus* and *B. luciae* were described by Rasolonjatovo et al. (2010). We re-describe these species because of the bad condition of the voucher specimens and/or the deficiency of some data in the previous descriptions. For having that would have mad a suitable comparison difficult. The same tadpole specimen of *B. englaenderi* from Marojejy National Park was redescribed to facilitate the comparison to the other *B. luteus* group tadpoles. We described the tadpoles of *B. vittatus* and *B. luciae* from the same locality based on new voucher specimens because of the bad condition of the voucher used in Rasolonjatovo et al. (2010).

In this study, fourteen new descriptions of tadpoles are provided, *B. englaenderi* [Ca45; Vieites et al. 2009], *B. albipunctatus, B. sambirano*, *B. mandraka* [Ca38], *B. mandraka* [Ca46], *B. sambirano* [Ca47], *B. sambirano* [Ca48], *B. sambirano* [Ca49], *B. sambirano* [Ca50], *B. marojezensis* [Ca25], *B. marojezensis* [Ca26], *B. marojezensis* [Ca51], *B. marojezensis* [Ca52], and *B. marojezensis* [Ca53].

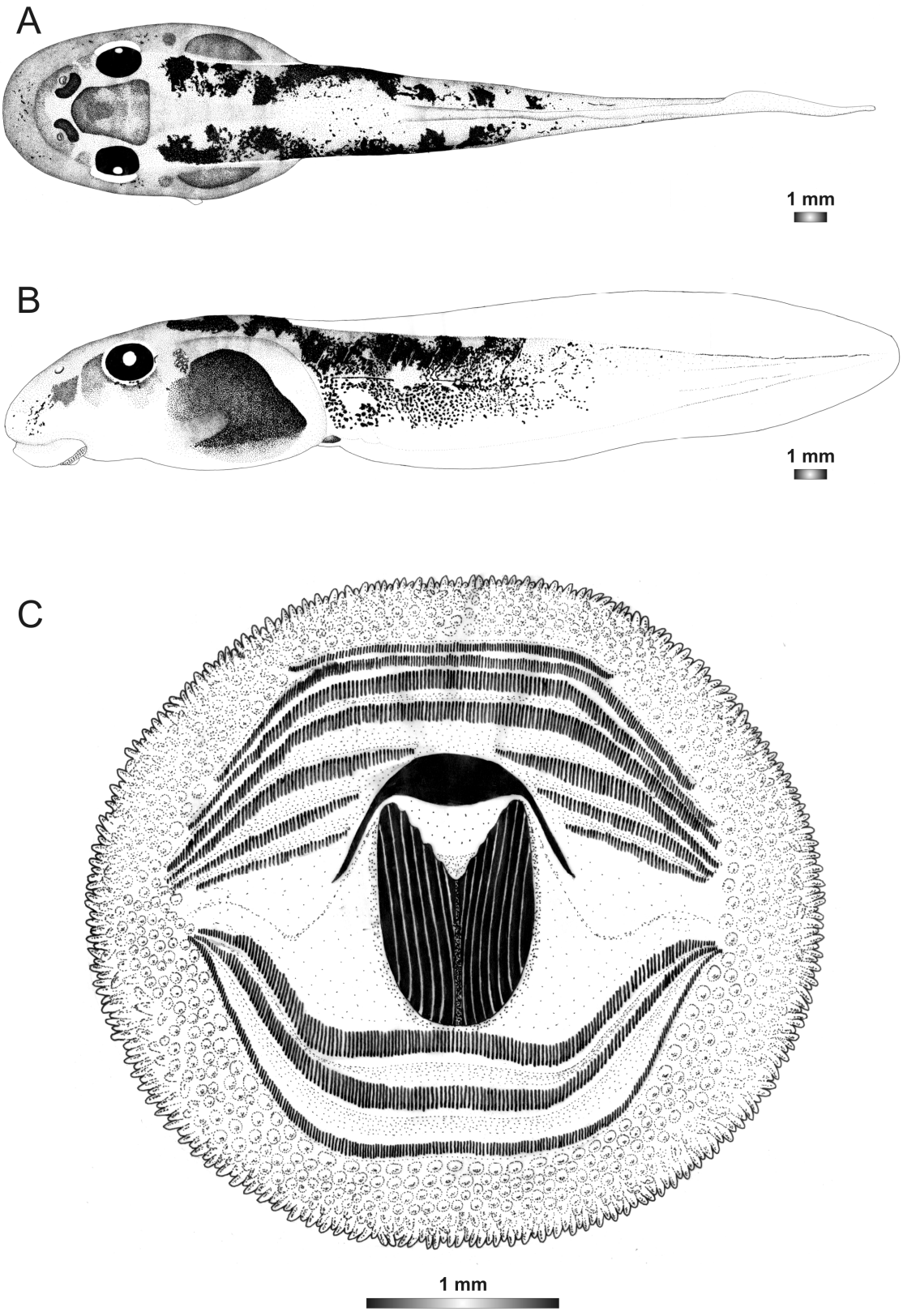

Figure 22. Drawings of the preserved DNA voucher tadpole of *B. marojezensis* [Ca52] (ZCMV 13168 - ZSM 541/2010): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

2. Morphological differences among tadpoles of closely related species

As described by Blommers-Schlösser (1979), defined by Raharivololoniaina et al. (2006), confirmed by Glos et al. (2007) and observed herein, strongly rheophilous tadpoles are typical stream-inhabiting species, and are characterized by the narrow and flat elongated body, the well developed caudal musculature, the wide oral disk with many small papillae that are either complete or interrupted by a dorsal gap, a rather small and ribbed (*i.e.*, composed of a series of fused columns) lower jaw sheath, many upper lateral tooth rows with at least the two first being uninterrupted and three lower tooth rows which in most of the species the first one is uninterrupted. This type of tadpoles can be found in different *Boophis* species groups: *B. luteus* group, *B. albipunctatus* group, *B. mandraka* group, *B. majori* group and *B. rappiodes* group. As described by Blommers-Schlösser (1979) and Schmidt et al. (2008), *B. williamsi* (*B. microtympanum* group) has also an enlarged oral disk (ODW 90% of BW, pers obs.) with a LTRF of 8(3-8)/3. However, we exclude it in our study because of the fact that *(1)* these tadpoles have a generalized oral disk structure (jaw sheaths, papillae and keratodonts) and *(2)* all the other strongly rheophilous tadpoles have a rather small size (BL 5.9 – 13.5 mm, TL 12.7 – 27.1 mm, in Gosner stages 25 – 36) compared to *B. williamsi* tadpoles (BL 25.5 mm and TL 71.7 mm in Gosner stage 36), which, as a high mountain species, might still get larger later in development.

Within the main groups of morphologically similar tadpoles, some can be very similar, but usually there are morphological details to differentiate them, whether in the external morphology or in the oral disk configuration; *i.e.*, tadpoles that are very similar in external morphology can be differentiated in oral disk structure and vice versa:

(1) Three tadpoles belonging to the *Boophis luteus* group (*B. englaenderi, B. englaenderi* [Ca45], and *B. andohahela*) look alike in external morphology but can be differentiated easily by their lateral tooth row formula. *B. englaenderi* and *B. englaenderi* [Ca45] occur syntopically. The tadpoles of *B. englaenderi* [Ca45] can be distinguished from those of *B. englaenderi* by their relative tail length, by their pigmentation pattern, and mainly by their oral disk structure (LTRF and number of papillae).

(2) In the *B. albipunctatus* group; *B. ankaratra*, *B. schuboeae*, *B. sibilans*, and *B. luciae* are similar. *B. ankaratra* and *B. schuboeae* occur sympatrically, and they can be differentiated by the presence of a dark pigmented band on the tail muscle and also by the absence of papillae on the lateral area where the oral disk folds in *B. schuboeae*. *B. sibilans* and *B. luciae* live allopatrically, and *B. luciae* differs to *B. sibilans* by the presence of a dark bridge which connects the dark sections on the tail muscle.

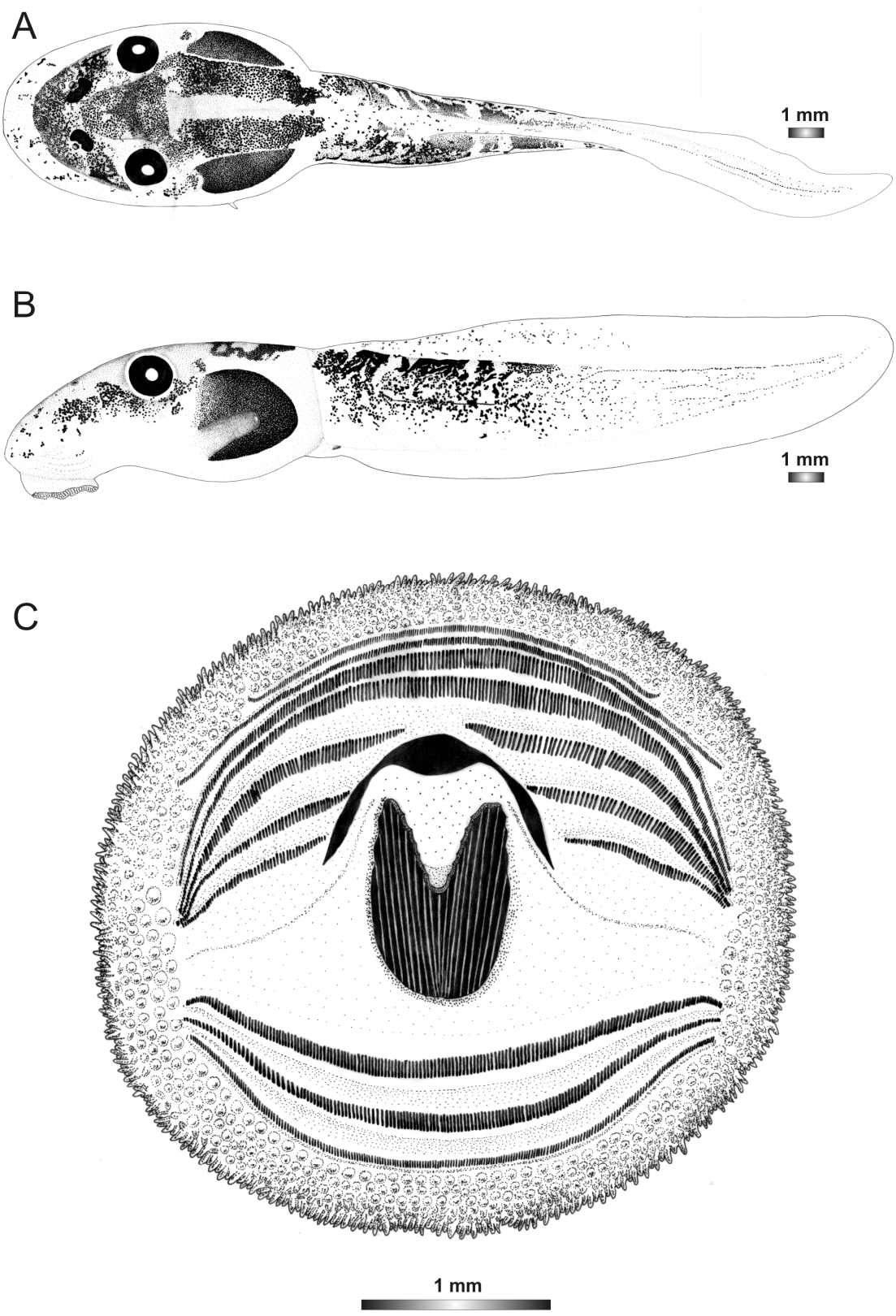

Figure 23. Drawings of the preserved DNA voucher tadpole of *B. marojezensis* [Ca53] (ZCMV 13200 - ZSM 573/2010): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

(3) All tadpoles known from the species of *B. mandraka* group have a similar oral disk configuration, characterized by the absence of the upper jaw sheath and the LTRF of 8(6-8)/3. The tadpoles of *B. sambirano* and *B. mandraka* [Ca46] are very similar, except that *B. mandraka* [Ca46] have the narrowest dorsal gap of marginal papillae. The fact that these two tadpoles live allopatrically can help also to identify them. Five species of this group are closely distributed in the North of Madagascar, *B. sambirano* [Ca47] and *B. sambirano* [Ca48] are sympatric, and can be differentiated by the patched pattern on the tail (spotted in *B. sambirano* [Ca48]). *B. sambirano* [Ca49] and *B. sambirano* [Ca50] live also sympatrically. *B. sambirano* [Ca49] can be distinguished to the three other species by its generally dark coloration pattern, the ovoid form of the body in dorsal view and the wide inter-orbital distance. *B. sambirano* [Ca50] can be differentiated by the intensity of the golden pigment which may cover the whole body and may cover the dark pigment in some specimens. *B. mandraka* [Ca38] is very typical by its weak state of pigmentation.

(4) Two tadpoles belonging to two different groups, *B. albipuncatus* (*B. albipunctatus* group) and *B. mandraka* [Ca38] (*B. mandraka* group) are similar in their weak pigmentation pattern. They can easily differentiated by their oral disk morphology. These species can occur syntopically.

(5) Two cases of similarity are also found in *B. majori* group tadpoles. *B. marojezensis, B. marojezensis* [Ca26], *B. marojezensis* [Ca53] and *B. vittatus* are very similar in the presence of a clear, not pigmented lateral area surrounding the body, and in the tail pigmentation pattern. The fact that they can occur sympatrically increases also the chance to confound them. On the other hand, the tadpoles of *B. marojezensis* [Ca51] and *B. marojezensis* [Ca52] are similar in the invisibility of the lateral clear area surrounding the body and in their general pigmentation pattern. Only the tadpole of *B. marojezensis* [Ca25] is easily distinguishable by the presence of clear and more or less rounded patches on the tail muscle. As the three *B. marojezensis*-like tadpoles, *B. marojezensis*, *B. marojezensis* [Ca25] and *B. marojezensis* [Ca26], live syntopically in Marojejy National Park, *B. marojezensis* [Ca25] tadpoles will not be confounded to those of the two other species.

3. Evolution of the strongly rheophilous *Boophis* tadpoles

Analyzing the structure of the oral disk of all these tadpoles allows classifying them into three clusters:

(1) The first cluster including three *B. luteus* group tadpoles is characterized by a moderately wide to very wide oral disk (ODW 56 to 84% of BW), non emarginated, ventral positioned and oriented oral disk which has an anterior margin connected directly to the snout, two uninterrupted upper rows of keratondonts (LTRF is 6(3-6)/3(1) for *B. englaenderi* but 6(3-6)/3 for the tadpoles of *B. englaenderi* [Ca45] and *B. andohahela*), a very long A_1 (82 to 90% of ODW),

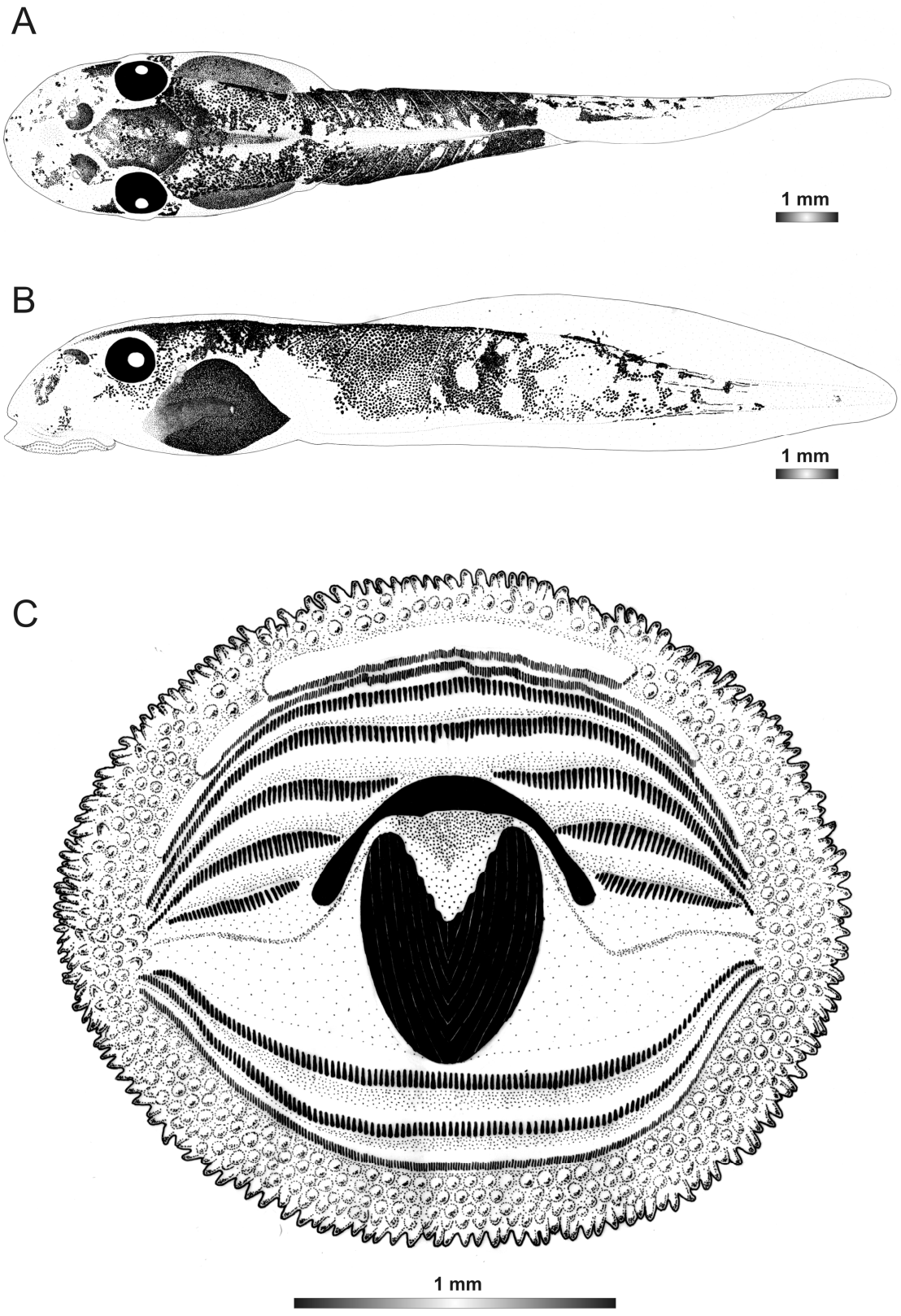

Figure 24. Drawings of the preserved DNA voucher tadpole of *Boophis vittatus* (FGZC 2238 - ZSM 1906/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

a high number of keratodonts in A_1 (220 to 301), totally keratinized, typically narrow to moderate sized jaw sheaths (JW 31 to 46% of ODW), a very short medial convexity (MCL 0.04 to 0.11% of JW), a wide to very wide dorsal gap of papillae (DG 67 to 85% of BW), a low number of submarginal papillae (33 to 94) and a medium number of marginal papillae (101 to 175), a high positioned eye (EH 69 to 85% of BH) that is situated not far from mid-body (SE 32 to 39% of BL), very high positioned nares (NH 57 to 82% of BH) which are situated below or at eye level (NH 82 to 97% EH) and closer to the snout than to the eye (RN 60 to 92% of NP), a short tail (TAL 155 to 183% of BL), and a developed caudal musculature.

(2) The second cluster is characterized by a wide to hyper-wide (ODW 74 to 108% of BW) non emarginated, ventral positioned and oriented oral disk with an anterior margin separated from the snout by a shallow crevice or free, four or five uninterrupted upper rows of keratondonts giving the LTRF 7(5-7)/3 or 8(6-8)/3, a short to moderately sized A_1 (21 to 59% of ODW), a low to medium number of keratodonts in A_1 (95 to 241), a totally keratinized, narrow upper jaw sheaths (JW 30 to 34% of ODW which can present a short medial convexity or not), a U-shaped and ''ribbed'' – giving the appearance of vertical bars – lower sheath, a moderately wide to very narrow dorsal gap of papillae (DG 14 to 59% of BW), a medium to high number of marginal papillae (148 to 377), many submarginal papillae (190 to 368), high to very high positioned eyes (EH 71 – 84% of BH) that can be situated closer to midbody (SE 35 to 49% of BL), high to very high positioned nares (NH 64 to 92% of BH) that are situated below, at or above eye level (NH 86 to 112% of EH) and closer to the eye than to the snout (RN 107 to 194% of NP), a very short to short tail (TAL 146 to 184% of BL), and a developped caudal musculature. Tadpoles of the *B. albipuncatus* group (*B. schuboeae*, *B. ankaratra*, *B. albipunctatus*, *B. sibilans*, and *B. luciae*) and *B. mandraka* group (*B. sambirano*, *B. mandraka* [Ca38], *B. mandraka* [Ca46], *B. sambirano* [Ca47], *B. sambirano* [Ca48], *B. sambirano* [Ca49], and *B. sambirano* [Ca50]) belong to this group. All *B. mandraka* group tadpoles have no keratinized upper jaw sheath.

(3) The third cluster is characterized by a wide (ODW 68 to 79% of BW) non emarginated, ventral positioned and oriented oral disk without a dorsal gap of papillae and with the anterior margin being free from the snout, four uninterrupted upper tooth rows (LTRF 7(5-7)/3), a moderately sized A_1 (45 to 52% of ODW), a medium number of keratodonts in A_1 (126 to 235), a totally keratinized, narrow upper jaw sheaths (JW 30 to 38% of ODW) without medial convexity, a U-shaped and ribbed lower sheath, many submarginal (222 to 318) and marginal (206 to 522) papillae, high positioned eyes (EH 68 to 80% of BH) that are situated closer to midbody (SE 35 to 49% of BL), very high positioned nares (NH 68 to 80% of BH) that are situated just below eye level except for *B. vittatus* and *B. marojezensis* [Ca25] (NH 89 to 101% of EH) and closer to the snout for the most (RN 78 to 109 % of NP), a very short to short tail (TAL 140 to 188% of BL), and a developed caudal musculature. Tadpoles of *Boophis majori* group

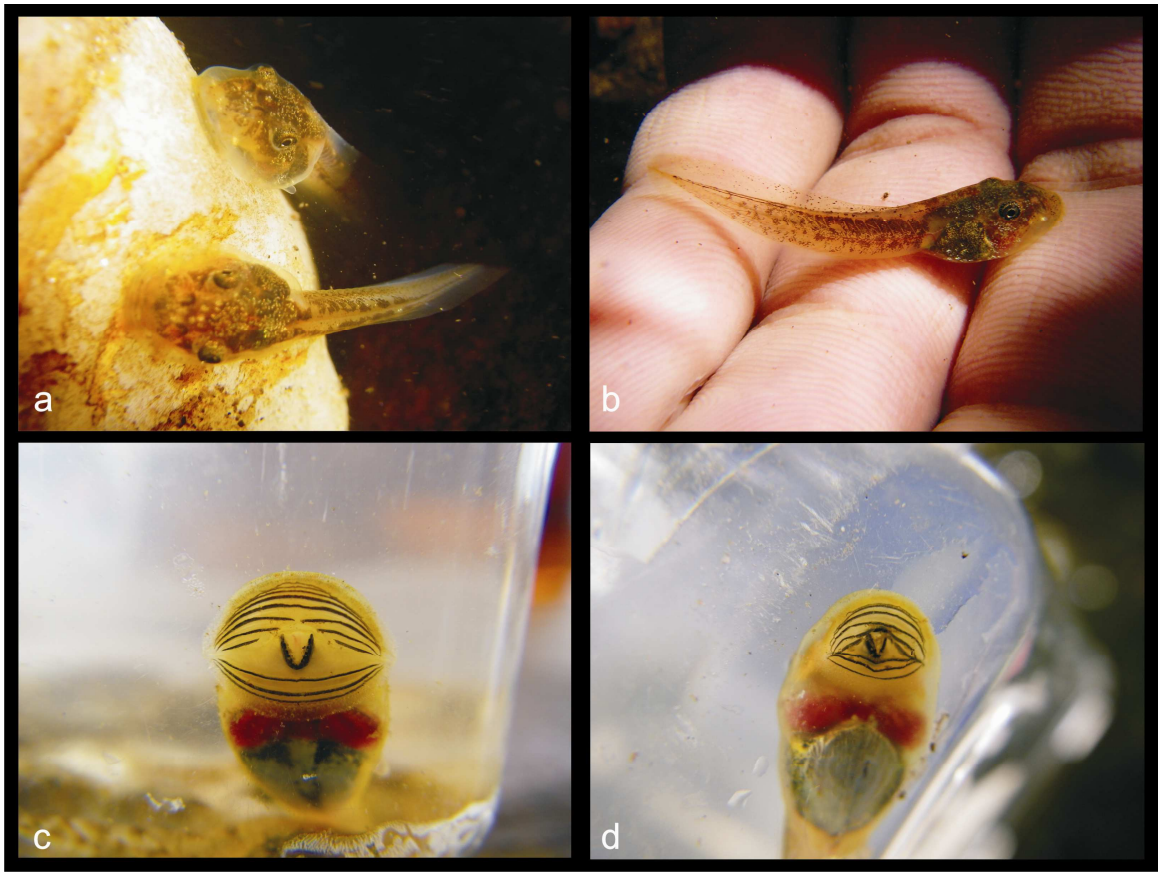

Figure 25. Photographs in life of strongly rheophilous *Boophis* tadpoles: **a** and **b** – Underwater pictures of *B. sambirano*-like tadpoles (from Antevialambazaha - Tsaratanana Integral Reserve); **c** and **d** – Oral disk of *B. sambirano* [Ca48] (ZCMV 13109 - ZSM 485/2010) and *B. marojezensis* [Ca52] (ZCMV 13169 - ZSM 542/2010) (from Ambinanitelo) fixing on the sides of an aquarium.

(*B. marojezensis*, *B. marojezensis* [Ca25], *B. marojezensis* [Ca26], *B. marojezensis* [Ca51], *B. marojezensis* [Ca52], *B. marojezensis* [Ca53], and *B. vittatus*) belong to this group.

An evolutionary trend from the generalized to the strongly rheophilous tadpoles is found in the first and second cluster. All generalized tadpoles are characterized by having one (the first) uninterrupted upper tooth row and one (the first) interrupted lower tooth row, typically smooth surfaced jaw sheaths, and a medial convexity in the upper jaw sheath (see Raharivololoniaina et al. 2006; Randrianiaina et al. 2009a, b; and Rasolonjatovo et al. 2010). Consequently, the presence of two uninterrupted upper tooth rows indicates an evolutionary trend towards an enlarged oral disk. Accordingly, the presence of a first lower interrupted row means that the oral disk still shows this characteristic of generalized tadpoles, and thus larvae of *B. englaenderi* stand in the itinerary of the process that leads towards this enlargement. In addition, common characteristics showing this tendency in this group are the state of the anterior margin of the oral disk which is still connected to the snout, and the presence of a medial convexity of the sheath in all species of this group. In brief, it is important to notice that the external morphology of the tadpoles in the first group shows no great differences, and they also belong together in the same species group of *B. luteus*. The presence of the medial convexity on the upper sheath on one hand, and the anterior margin of the oral disk which is connected directly to the snout on the other hand is also found in two species (*B. schuboeae* and *B. ankaratra*) of the second group; however, these species already have a ribbed lower sheath and an elevated number of uninterrupted upper tooth rows.

According to the characteristics of the three groups, the following evolutionary scenario for the evolution of this type of oral disk can be drawn: There are reductions of *(1)* the size of the jaw sheaths (with *(2)* the disappearance of the medial convexity), *(3)* the size of the dorsal gap of marginal papillae, *(4)* the length of the A_1 row, *(5)* the number of keratodonts in A_1, compensated by an increase of the number of *(6)* marginal and *(7)* submarginal papillae, and *(8)* the uninterrupted upper tooth rows.

The decrease of the size of the jaw sheaths provokes the fading of its medial convexity on one hand and leaves a place for many dorsal and lateral, even ventral submarginal papillae, and new uninterrupted upper tooth rows on the other hand. Also, the reduction of the size of the dorsal gap leads to a higher number of marginal papillae. The development of many dorsal marginal papillae reduces the area available for the first upper tooth row and causes the diminution of its length, which in turn leads to the decrease of the number of the teeth. However, the loss of the upper jaw sheath in all species and candidate species of the *B. sambirano* complex is still unclear. This characteristic is neither caused by a fixation artefact nor by the transportation of the specimens as it was already observed in living tadpoles. All tadpoles within the same series show the same characteristics. This morphology was found even in young tadpoles

Figure 26. Pictures showing tadpoles capture sites inside a primary forest in Ranomafana National Park with almost closed canopy cover **a** – in Fompohonina river and **b** – in Piste E 100 stream, and outside the forest **c** – in Anjingo river and **d** – in Ankijagna Lagnana.

(Gosner 25) indicating that the loss of the upper jaw sheath occurs very early in the larval development. It remains to be tested (*e.g.*, by a study on embryonic development), however, if this structure is never developed throughout embryonic development or if it disappears when the tadpoles hatch.

4. Ecomorphological guilds in *Boophis* tadpoles

A magnitude of descriptions of the larval stages of Madagascan frogs have been recently published (Andreone et al. 2002; Glos & Linsenmair 2005; Raharivololoniaina et al. 2003, 2006; Thomas et al. 2005, 2006; Altig & McDiarmid 2006; Vejarano et al. 2006a, b, c; Grosjean 2006, 2007; Glos et al. 2007; Randrianiaina et al. 2007, 2009a, b; Schmidt et al. 2008, 2009a, b; Grosjean & Vences 2009; Jovanovic et al. 2009; Rasolonjatovo et al. 2010). While some of them are merely intended to increase general knowledge on Madagascan tadpoles, others attempted to classify the tadpoles into ecomorphological guilds. For *Boophis* tadpoles, Raharivololoniaina et al. (2006) tried to define three guilds, named A, B, and C, mainly based on three variables: relative width of oral disk, number of inframarginal papillae, and number of keratodonts on the first anterior row. As already mentioned by Randrianiaina et al. (2009a), these guilds were not intended to replace nor to refine the guilds of Altig & Johnston (1989), but to achieve a complementary, more quantitative classification that would better fit the variation in *Boophis* tadpoles. Moreover, the criteria chosen by Raharivololoniaina et al. (2006) were too few and some of those that Altig & Johnston (1989) used do not exist in *Boophis* tadpoles (Randrianiaina et al. 2009a). Therefore, the definition of adequate guilds for Malagasy tadpoles requires including many new variables, without omitting those that have been used before. Accordingly, it is very important to notice first the presence or absence of one component (*e.g.*, jaw sheath and keratondont) and then its configuration (*e.g.*, totally or poorly keratinized sheaths, density of papillae; Randrianiaina et al. 2011).

In this study we intended only to give an overview of the guild of strongly rheophilous tadpoles. Defining appropriate guilds for this genus necessitates a complete data set of all described larval stages; however, all previously published studies did not provide the appropriate data for this aim. According to Altig & Johnston (1989), three different guilds might correspond to *Boophis* tadpoles. The clasping tadpoles have a dorsal gap of marginal papillae, commonly five labial tooth rows (but as numerous as 8/8), usually with anterior rows that are more numerous than posterior rows (*e.g.*, 9/3), and a globular to slightly depressed body. They inhabit medium to slow water currents and the maintenance of their position in the water current with the help of the oral disk is of minor importance. The adherent tadpoles have small and complete marginal

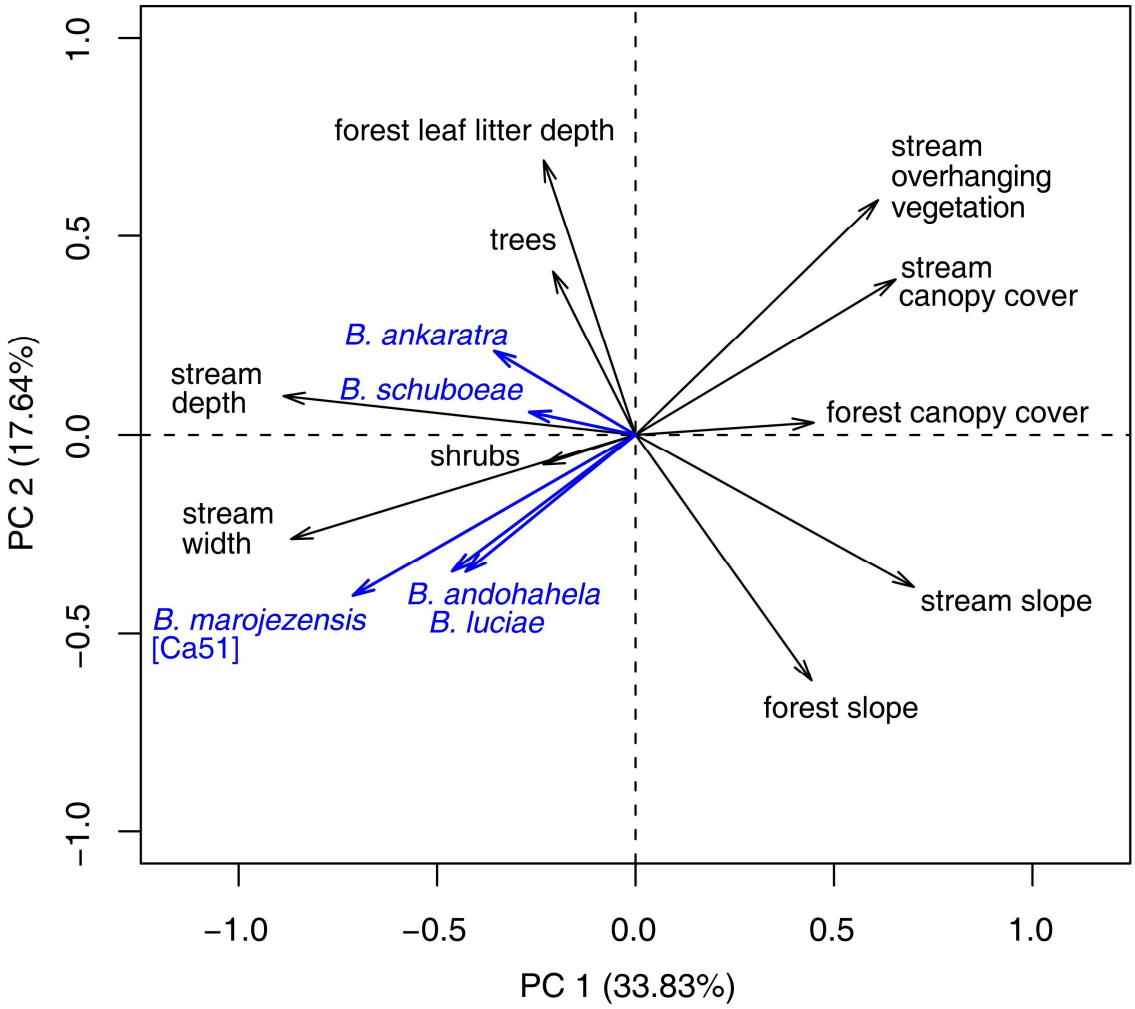

Figure 27. PCA biplot of variables of stream and surrounding habitat as recorded during a tadpole community study in Ranomafana National Park. The five present species of strongly rheophilous tadpoles are included as supplementary variables. Length and direction of vectors can be interpreted as correlations.

papillae, and a LTRF of commonly 2/3. They inhabit faster flowing water than clasping tadpoles, their position maintenance via the oral disk is common to continuous, and their body is often depressed. The suctorial tadpoles have a depressed body, small and complete marginal papillae, and a LTRF from 2/3 to a maximum of 17/21. They inhabit even faster running waters than clasping and adherent tadpoles, and their position maintenance via their oral disk is continuous.

In this study, no new guild name will be defined, but we are going to adapt the guilds already defined by Altig & Johnston (1989) into our tadpole system. Considering *B. luteus* group tadpoles as being not a part of the strongly rheophilous tadpoles, due to their basal generalized and intermediate characteristics, two guilds of strongly rheophilous tadpoles are considered:

(1) The first guild that we define as "adherent" is the second category of tadpoles classified in the previous section which is composed by the tadpoles of the *B. albipuncatus* group (*B. schuboeae*, *B. ankaratra*, *B. albipunctatus*, *B. sibilans*, and *B. luciae*) and the *B. mandraka* group (*B. sambirano*, *B. mandraka* [Ca38], *B. mandraka* [Ca46], *B. sambirano* [Ca47], *B. sambirano* [Ca48], *B. sambirano* [Ca49] and *B. sambirano* [Ca50]), because they inhabit faster running water and the maintenance of the position in the water via their oral disk is common to continuous by the presence of noumerous papillae combined with dorsal gap of papillae. This guild is characterized mainly by the presence of a dorsal gap of papillae and two typical LTRF's which are 8(5-8)/3 and 8(6-8)/3. All *B. mandraka* group tadpoles loose their upper sheath, while all *B. albipuncatus* group tadpoles keep their upper sheath.

(2) The second guild that we define as "suctorial" is the third category of tadpoles classified in the previous section which is composed of all *B. marojezensis*-like (*B. marojezensis, B. marojezensis* [Ca25], *B. marojezensis* [Ca26], *B. marojezensis* [Ca51], *B. marojezensis* [Ca52], *B. marojezensis* [Ca53], and *B. vittatus*) tadpoles. They inhabit faster running water and maintain continuously their position in the water with the help of their oral disk because of the complete state of the papillae that they have. This guild is characterized by the absence of a dorsal gap of papillae and a LTRF of 7(5-7)/3.

Ecomorphological guild assignment supposedly is closely correlated to microhabitat choice and resource use. Accordingly, our preliminary results on gut content analysis reveal a large difference in algae quantity between *B. schuboeae* and *B. marojezensis* [Ca51]. This indicates that tadpoles use differently the resource according to the configuration of the oral disk. And this fact supports the classification of the two forms of oral disk into two different guilds.

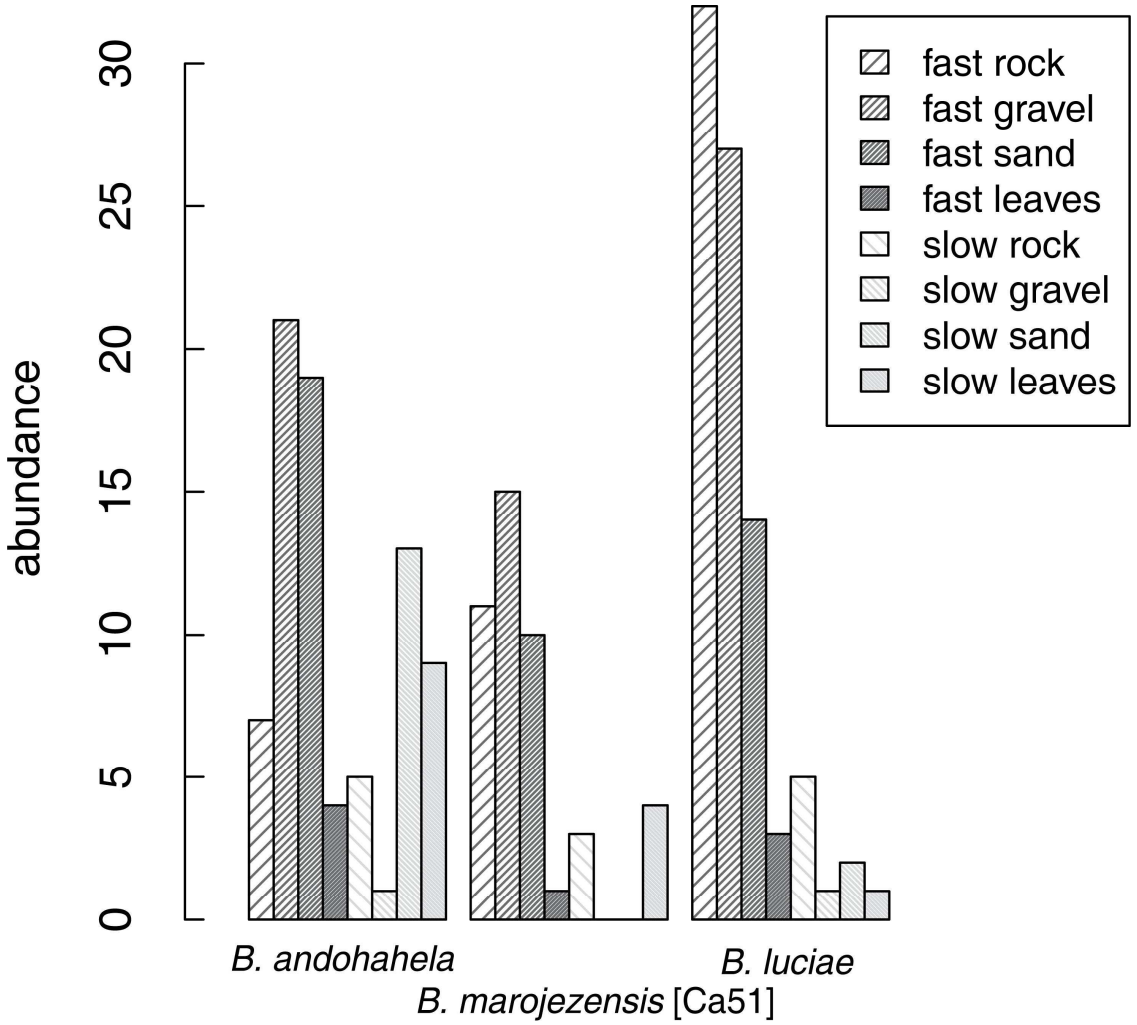

Figure 28. Tadpole distribution across the 8 microhabitats (defined using water current and stream substrat); of the three most abundant strongly rheophilous *Boophis* that were sampled in Ranomafana National Park in wet season 2008. *B. andohahela*: N=8, *B. marojezensis* [Ca51]: N=7, *B. luciae* N=10 with N= the number of streams.

5. Habitat selection and ecology of strongly rheophilous *Boophis* tadpoles

In the tropical rainforest of RNP, strongly rheophilous *Boophis* tadpoles occur throughout the whole year (own unpublished data) with clearly higher abundances in the wet season. Whereas some species are relatively common (*e.g.*, *B. andohahela*, *B. marojezensis*, and *B. luciae*), others are locally extremely rare (*e.g.*, *B. ankaratra*, *B. schuboeae*). In this area, strongly rheophilous *Boophis* do neither include the most common tadpoles species nor is the group itself as common as other groups (Grosjean et al. 2011). Species of this group choose larger, open, slowly running streams for breeding; small streams with high slope and a dense vegetation cover are generally avoided. This is generally true for all strongly rheophilous species studied in Ranomafana National Park. The latter kind of stream might be avoided as they are less attractive to adults than large streams, which provide more space without the risk of egg- and tadpole predation by fishes. Small streams can also be characterised by reduced food availability; *e.g.*, due to reduced periphyton growth as a result of high vegetation coverage (Mallory & Richardson 2005; Altig et al. 2007). This actually describes the expected pattern for most tadpoles in Madagascan rainforest streams and can also be observed; *e.g.*, for tadpoles of the *Mantidactylus* subgenus *Ochthomantis*, which are characterised by reduced oral disk structures (Randrianiaina et al. 2011). In contrast, the also specialized funnel mouthed tadpoles of *Mantidactylus* subgenus *Chonomantis* do not follow this pattern, as for some species, no prediction of occurrence by habitat characteristics is possible and some species (*e.g.*, *Mantidactylus opiparis*) prefer combinations of habitat characteristics that are unfavourable represented in our PCs (Grosjean et al. 2011).

Within the streams, however, strongly rheophilous *Boophis* tadpoles are quite outstanding regarding their microhabitat choice compared to other abundant and well observed tadpoles groups. This is especially true for two of the most common of these species, *B. marojezensis* [Ca51] and *B. luciae*, and less pronounced for *B. andohahela*, as this last one does not belong not to adherent or suctorial tadpole guilds because of its generalized oral disk structure. Whereas we could not show true preferences for fast running sections, we could at least show that a considerable number of specimens are indeed using these faster parts of the streams. This clearly separates these tadpoles from other abundant groups (Grosjean et al. 2011; Randrianiaina et al. 2011), and is most likely due to the morphological specialisations of oral disk, body, and tail to withstand the current.Their large ventral oral disk allows attaching on substrate (Figure 25) such as rocks and gravel, and the presence of numerous short papillae presumably aids in forming a tight seal between the oral disk and the irregularities of substrate (Altig & McDiarmid 1999a). Also, their relatively small body size and well developed caudal musculature causes a good performance in strong current.

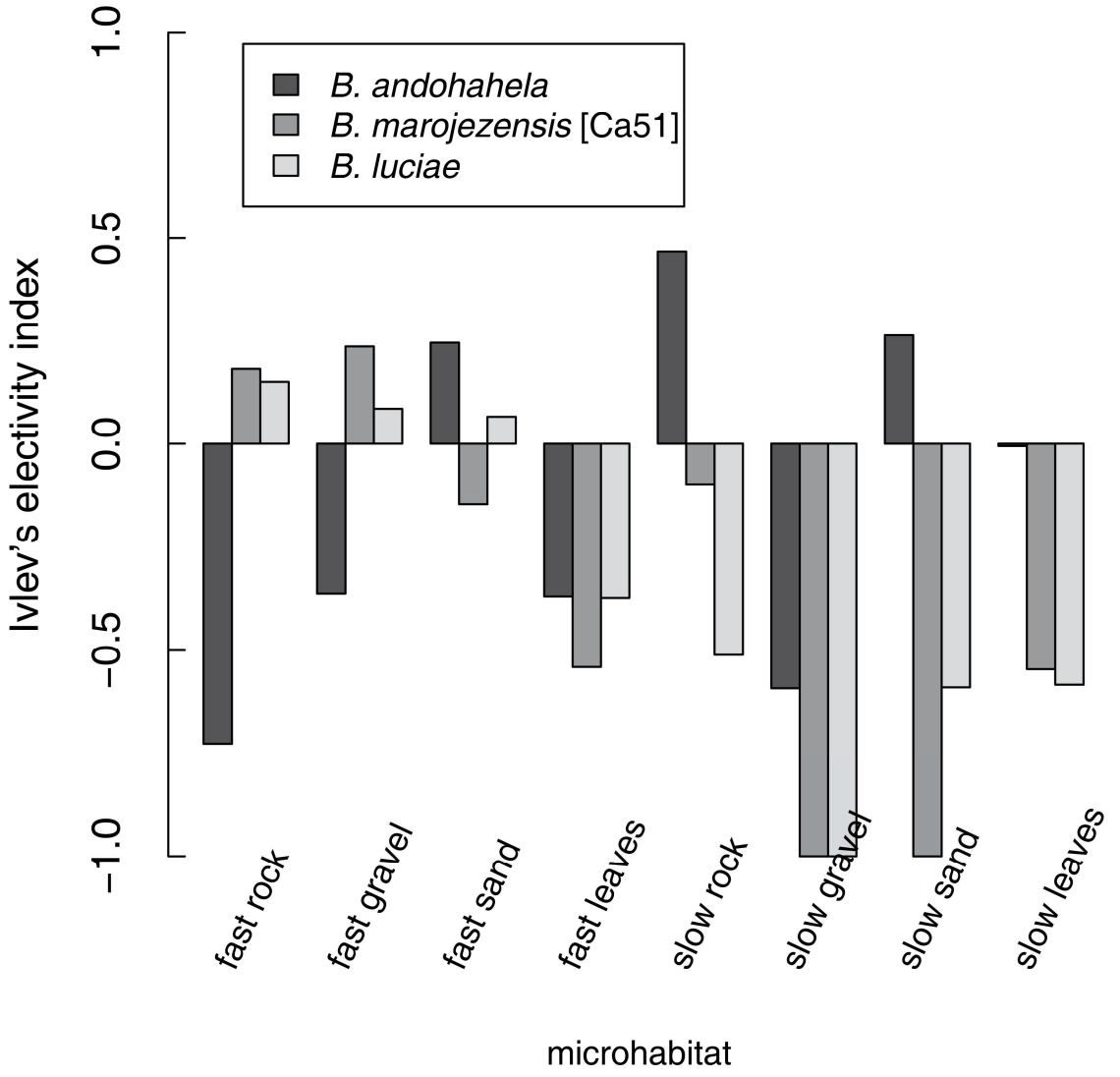

Figure 29. Barplot displaying microhabitat use of three most abundant *Boophis* species with strongly rheophilous tadpole form. Microhabitat use is calculated using Ivlev's electivity index (E, Ivlev 1961) with positive values representing microhabitat preferences and negative values representing microhabitat avoidance. For each species, only streams with at least 8 specimens were used for analysis (*B. andohahela*: N=3, *B. marojezensis* [Ca51]: N=2, *B. luciae*: N=4 with N= the number of streams).

6. Phylogeny

Not all stages of evolution are seen within one species group of *Boophis*, and it seems that the enlargement of the oral disk evolved independently in different species groups; *i.e.*, this morphology evolved convergently. An early stage of the increase of the number of uninterrupted tooth rows is found in *B. luteus* group tadpoles. The *B. luteus* group represents the beginning of the evolution of a generalized oral disk into an enlarged oral disk as its tadpoles have generalized non emarginated oral disks (Raharivololoniaina et al. 2006; Randrianiaina et al. 2009a; and Rasolonjatovo et al. 2010). The intermediate stages characterized by the reduction of jaw sheath size, the reduction of dorsal gap size, an increasing number of uninterrupted tooth rows, and an increasing number of papillae are found in the *B. albipunctatus* group and *B. mandraka* group. The final stage of evolution is then found in *B. majori* group tadpoles.

As already demonstrated in Randrianiaina et al. (2011), reverse taxonomy can also be applied to better studied groups such as vertebrates. Herein we confirm the usefulness of this method by finding numerous divergent tadpole DNA sequences. Twelve candidate species are defined in this study by the divergent DNA sequence of the tadpoles in comparison with the adult sequence. As the syntopic occurrence is an important factor in Padial's scheme (Padial et al. 2010), a close morphological examination of sympatrical tadpoles was realised to understand if they are really different species. Such morphological difference in tadpoles has already been used to distinguish two cryptic treefrogs, *Boophis boehmei* and *Boophis quasiboehmei* (Randrianiaina et al. 2009b and Vences et al. 2010) and it was already prominent to differentiate two different sympatrically occurring tadpoles, *B. ankaratra* and *B. schuboeae* (Glos et al. 2007).

After examining the sympatrical form, we assess three of them as Confirmed Candidate species (CCS) exclusively based on tadpole characters:

(1) B. englaenderi [Ca45] lives syntopically with *B. englaenderi* and both show clear and constant differences. All tadpoles assigned to *B. englaenderi* [Ca45] have an oral disk with lateral bulges, a LTRF of 7(3-7)/3 and a high number of papillae, although it is not bulged in *B. englaenderi* and the submarginal papillae are positioned laterally only. *B. englaenderi* [Ca45] tadpoles have also a rather long tail in comparison with those of *B. englaenderi*. The pigmentation pattern is also very different between the two species. *B. englaenderi* tadpoles are covered by dense dark reticulations on the body as well as on the tail, although *B. englaenderi* [Ca45] tadpoles have sparse clear reticulations, sometimes the spots just fused to form patches.

(2) In the *B. mandraka* group, *B. sambirano* [Ca49] tadpoles are very deviant and can easily be differentiated with its syntopical species, and even with all the tadpoles belonging to the same species group by the ovoid form of the body in dorsal view, the uniformly dark brown

pigmentation pattern, the non visibility of the lateral transparent area surrounding the body and the situation of the eyes between the 3/10 and 4/10 proximal of the body.

(3) B. marojezensis [Ca25] is very distinct by the presence of more or less rounded patches on the distal half of the tail musculature which make it easily do distinguish with its syntopical species *B. marojezensis* and *B. marojezensis* [Ca26].

This extraordinary and surprising diversity of *B. marojezensis*-like and *B. sambirano*-like candidate species in northern Madagascar claims for a biogeographic and evolutionary explanation, and confirms that stream-breeding frogs apparently show a higher geographical structuring of their diversity (*e.g.*, Vences et al. 2002). An in-depth revision of these frogs is necessary to understand this diversity and its taxonomic diversity, and needs to be based on an integrative approach assessing their bioacoustic, and nuclear genetic divergence, focusing on sympatric occurrences which we expect to be particularly informative regarding the isolation mechanisms between these lineages.

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Chapter 3

Sand-eating tadpoles in Madagascar: Morphology and ecology of the unique larvae of the tree frog *Boophis picturatus*

This chapter has been submitted to Salamandra on 11 January 2011 as follows:

Grosjean S, Randrianiaina RD, Strauß A & Vences M. 2011. Sand-eating tadpoles in Madagascar: Morphology and ecology of the unique larvae of the tree frog *Boophis picturatus*. Salamandra.

Abstract

Several anuran larvae of the family Mantellidae endemic to Madagascar and the Comoro islands have remarkable specializations, typically reflected in their derived mouthparts that often are characterized by a strong reduction of keratinized structures. While most of these specialized tadpoles are found in the genus *Mantidactylus*, the treefrogs of the genus *Boophis* typically have rather generalized tadpoles, with some lineages adapting to strong current by an enlarged oral disk with increased number of keratodont rows and papillae. A remarkable exception is *Boophis picturatus* which has an extremely derived oral disk without any labial teeth and completely reduced jaw sheaths and is known to ingest sand particles. We here provide a detailed description of the external morphology and buccal anatomy of this tadpole and provide evidence for constancy of this morphology in various localities in the southern central east and northern central east of Madagascar. We document that sand particles are mixed with organic matter in the anterior but not in the posterior part of the gut, suggesting they are being digested during their passage through the intestine. Ecologically *B. picturatus* tadpoles preferably occur in streams with a low slope in forest areas with high number of trees but less shrubs and thick leaf litter. No statistical microhabitat preference could be demonstrated but in the streams where the tadpoles occurred, sandy bottoms were by far the predominant substrate and most specimens were found on sand. The related *B. majori* that also show to a lesser degree derived mouthparts did not share the sand-eating behaviour of *B. picturatus*.

Key words: Amphibia, Mantellidae, Ranomafana National Park, tadpole morphology, buccal anatomy, clutches, habitat preference.

Introduction

Tadpoles, the aquatic larvae of frogs, are strikingly different from the terrestrial metamorphosed (juvenile as well as adult) frogs (Altig & McDiarmid 1999). Besides the general adaptation to aquatic life, the major differences are all related to the feeding behavior: while metamorphosed frogs are without exception carnivorous, most tadpoles are omnivorous suspension feeders (Altig & McDiarmid 1999), and have strongly modified mouthparts with numerous elements that are not homologous to any structures of the adult frogs or to the typical vertebrate *bauplan*. Nevertheless, the question what tadpoles really eat has been highlighted as one of the major question in herpetological research (Altig et al. 2007).

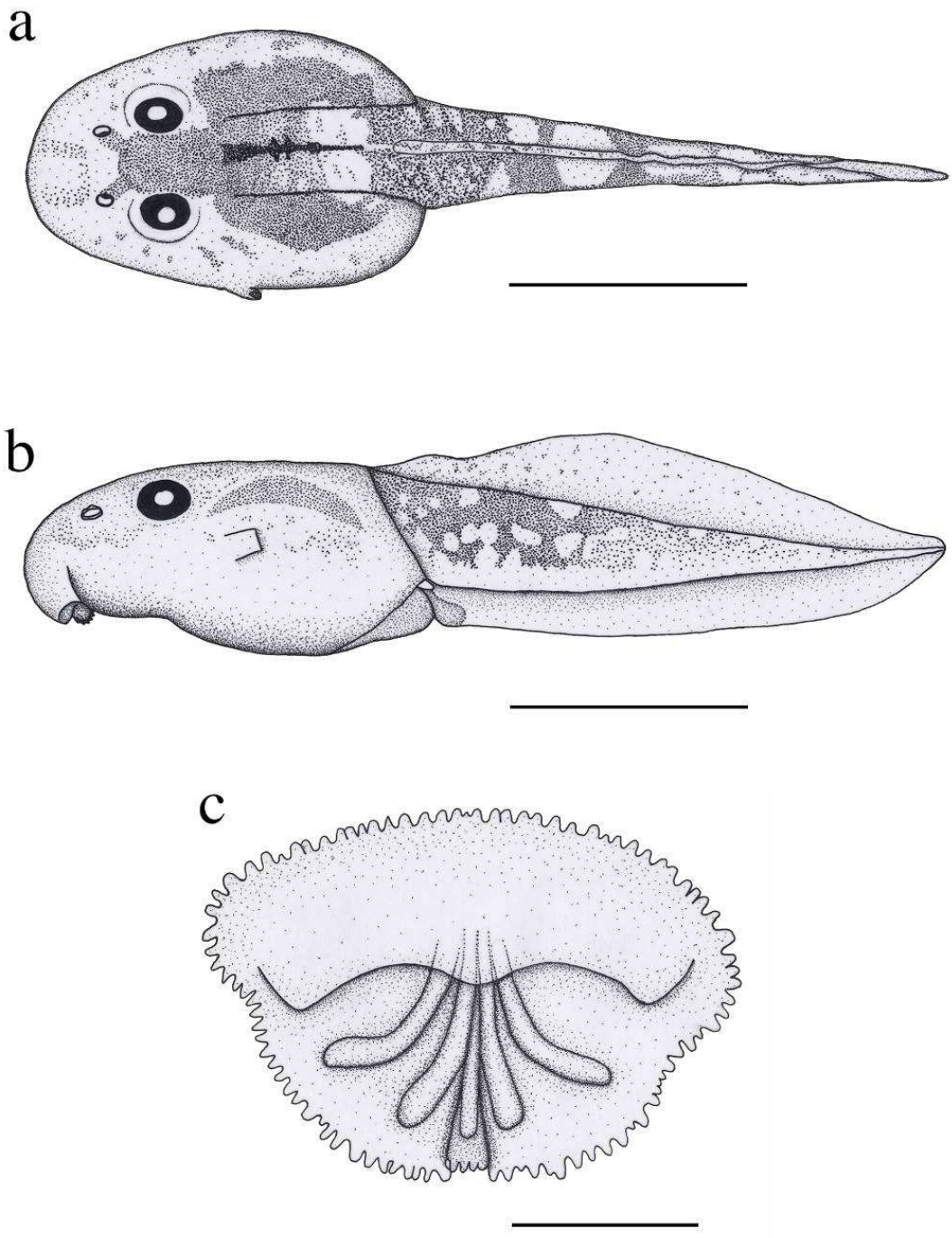

Figure 1. Drawings of *Boophis picturatus* tadpole: **a** – Dorsal, **b** – Lateral view of the of (ZSM 833/2004, stage 27, scale bar 10 mm), and **c** – oral disc of (ZSM 808/2004, stage 25, TL 18.3 mm, BL 7.7 mm, scale bar 1 mm). Note that the upper labium of the oral disc has been artificially lifted up to show the suprarostral. (Drawn by S. Grosjean)

Typically, tadpoles are characterized by an oral disc with keratinized jaw sheaths, and with equally keratinized labial "teeth" (also called keratodonts) which they use to rasp algae or bacterial films from underwater surfaces and ingest these particles. However, this typical tadpole morphology has been modified in multiple ways, and besides carnivorous tadpoles that usually reduce the keratodonts but develop stronger jaw sheaths, there are also tadpoles that have altogether reduced all of the keratinized oral structures in the course of evolution. In most cases, the natural history, feeding behaviour and food of these species are totally unknown. Three such remarkable tadpoles, all belonging into the endemic Malagasy-Comoran family Mantellidae, have been recently described by Altig & McDiarmid (2006). Most unusual, these authors reported that the tadpole of the treefrog *Boophis picturatus*, without any keratinized oral structures, is specialized to ingest sand.

During an intensive tadpole survey at Ranomafana National Park in the southern central east of Madagascar, and at several other localities on the island, we have been able to collect numerous tadpole specimens of *Boophis picturatus* and of two species (*Boophis majori* and *B.* sp. 35 (named *Boophis* sp. aff. *majori* "long calls" in Glaw & Vences 2007 and Schmidt et al. 2008) that molecular data place as close relatives of *B. picturatus* (Vieites et al. 2009) and that also show a trend of reduction of keratinized oral disc structures (Schmidt et al. 2008). We also systematically obtained data of the preferred microhabitat in the stream of these three species in the context of a wider ecological tadpole community study (*e.g.*, Strauß et al. 2010). In this paper, we complement previous data (Altig & McDiarmid 2006) on the *B. picturatus* tadpole by *(1)* describing its buccopharyngeal anatomy, *(2)* assessing genetic diversity and morphological uniformity among populations across its range, *(3)* provide an analysis of its microhabitat preferences based on data from Ranomafana, and *(4)* analyze and illustrate more in detail the intestine content of the species, comparing it to that of the tadpole of *B. majori*.

Material and Methods

1. Morphological and anatomical descriptions

Tadpoles were collected by different kind of nets having mesh sizes from 2 to 5 mm, depending on the size of the streams, the strength of the current and the type of substrate. They were euthanised by immersion in chlorobutanol solution, and immediately sorted into homogeneous series based on morphological characters. From each series one specimen was selected and a tissue sample from its tail musculature or fin taken and preserved in 99% ethanol. This specimen is here called

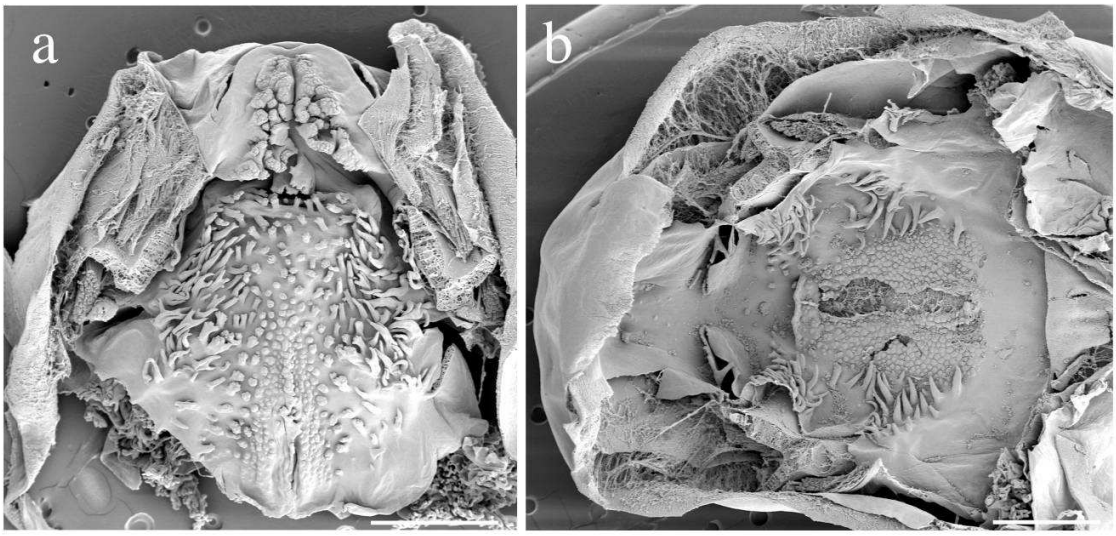

Figure 2. Scanning electron microscope pictures of the tadpole of *Boophis picturatus* (ZSM 808/2004, stage 25, BL 5.4 mm, scale bar 1 mm) showing the Buccal **a** – floor and **b** – roof.

"DNA voucher". All detailed morphological tadpole characterizations and drawings are based on this DNA voucher, whereas variation is described based on further specimens of the series. After tissue collection, all specimens were preserved in 5% formalin or 70% ethanol. Specimens were deposited in the Zoologische Staatssammlung München, Germany (ZSM). A total of 20 tadpoles at stages 25–37 from three localities (Ranomafana National Park, Fierenana, and Vevembe; collection numbers ZSM 808/2004, ZSM 821/2004 and ZSM 833/2004; see Appendix 2-Table 2) for geographical coordinates, dates, collectors) were examined. The specimens were deposited in the herpetological collection of the Zoologische Staatssammlung, München, Germany (ZSM).

Morphological terminology follows Altig & McDiarmid (1999) and developmental stages were determined according to Gosner (1960). Measurements were taken by SG with a graduated ocular attached to a stereomicroscope except for the total length which was measured with a hand caliper, and the tail length of the biggest specimens (from stage 27 on), to the nearest 0.1 mm. The landmarks are those shown in Altig & McDiarmid (1999: 26, Figure 3.1.), for other see Grosjean (2006). The abbreviations used in the description are the following: BH maximum body height; BL body length; BW maximum body width; ED maximum diameter of eye; LF maximum height of lower tail fin; MTH maximum tail height; NN internarial distance; NP naro-pupilar distance; ODW oral disc width; PP interpupilar distance; RN rostro-narial distance; SS distance from tip of snout to opening of spiracle; SU distance from snout to beginning of upper tail fin; TL total length; TMH maximum tail muscle height; TMW maximum tail muscle width; UF maximum height of upper tail fin.

Preparation for SEM examination (with a JEOL JSM-840A) comprised dehydration in a graded ethanol series, critical-point drying (liquid carbon dioxide) and gold sputter surface coating. Terminology of buccal structures follows Wassersug (1976).

In addition to the detailed morphological and anatomical study of the above-mentioned specimens, we provide morphological data for additional specimens from Ranomafana, An'Ala, Ambohitsara-Tsitolaka, and Fierenana; Table 1), and for these use the following abbreviations: A_1 first upper keratodont row, A_2 second upper keratodont row, A_{2gap} medial gap in row A_2, A_3 third upper keratodont row, A_4 fourth upper keratodont row, A_5 fifth upper keratodont row, $A_{1\text{-}5\ den}$ density of the keratodonts in row $A_{1\text{-}5}$, $A_{1\text{-}5\ len}$ length of the row $A_{1\text{-}5}$, $A_{1\text{-}5\ num}$ number of keratodonts in row $A_{1\text{-}5}$, DG size of the dorsal gap of marginal papillae, DMTH distance of maximal tail height from the tail-body junction, EH eyes height (measured from the lower curve of the belly), HAB height of the point where the axis of the tail myotomes contacts the body (measured from the lower curve of the belly), JW maximal jaw sheath width, MC medial convexity of the upper jaw sheath, MCL length of the medial convexity of the upper jaw sheath, MP marginal papillae, ND naris diameter, NH naris height (measured from the lower curve of the belly), OD oral disc, ODW maximum oral disc width, P_1 first lower keratodont row, P_2 second

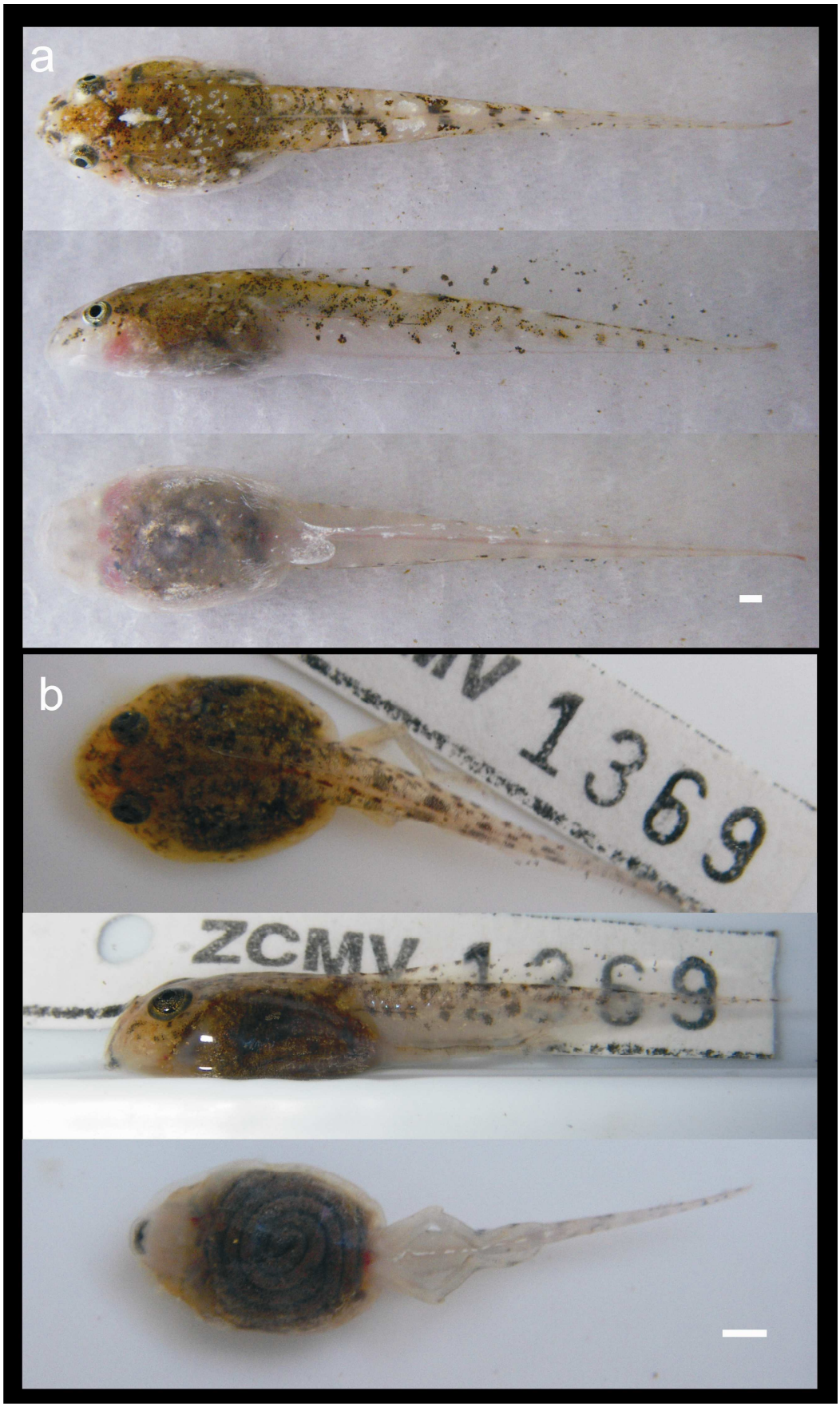

Figure 3. Photographs of living tadpoles of **a** – *Boophis picturatus* (T 08/0076 - uncatalogued) from Fompohonina IV (Ranomafana National Park) and **b** – *Boophis majori* (ZCMV 1369 - ZSM 37/2007) from Ankidoanavo (Ranomafana National Park). The scale bars represent 1 mm.

lower keratodont row, P_3 third lower keratodont row, $P_{1\text{-}3\ den}$ density of the keratodonts in row $P_{1\text{-}3}$, $P_{1\text{-}3\ len}$ length of the row $P_{1\text{-}3}$, $P_{1\text{-}3\ num}$ number of keratodonts in row $P_{1\text{-}3}$, (R/L) Right/Left, SBH distance between snout and the point of maximal body height, SBW distance between snout and the point of maximal body width, SE snout-eye distance, SH spiracle height (measured from the lower curve of the belly), SL spiracle length, SMP submarginal papillae, SV spiracle-vent distance, TAL tail length, TH tail height at the beginning of the tail, THM tail height at mid-tail, Thorn-pap thorn-shaped papillae, TMH tail muscle height at the beginning of the tail, TMHM tail muscle height at mid-tail, LR number of the lower rows of keratodonts, UR number of the upper rows of keratodonts, VG size of the ventral gap of marginal papillae, VL vent tube length, following Randrianiaina et al. (2011). These measurements (Table 2) were taken by RDR with a Zeiss StereoDiscovery V12 microscope with integrated digital camera connected to a computer.

Examination of the gut content was done by dissecting the belly skin. The gut was divided into two parts (front and rear) and the content of each part was observed separately. The gut content of the front part of *Boophis picturatus* was washed to examine the grains of sand (Fig. 07b). Three square plots of 9 mm^2 were photographed and maximum width of each grain of sand within this area was measured.

2. Molecular analysis

DNA barcoding was based on a fragment of the mitochondrial 16S rRNA gene, which is known to be sufficiently variable among species of Malagasy frogs (Vences et al. 2005). We amplified a fragment of ca. 550 bp using primers 16Sar-L and 16Sbr-H from PALUMBI et al. (1991), or a shorter fragment of ca. 400 bp using the newly developed specific mantellid primers 16S-Frog-L1 (CAT AAT CAC TTG TTC TTT AAA) and 16S-Frog-H1 (GAT CCA ACA TCG AGG TCG). PCR was carried out with standard protocols (Vences et al. 2005) and sequences resolved on automated sequencers. Sequences were preliminarily identified using BLAST searches against a near-complete database of sequences of adult Malagasy frog species. Results were subsequently verified by manually aligning and comparing sequences to the closest hits in the data base. Identification was considered to be unequivocal when the tadpole sequence was 99–100% identical to an adult specimen from the same geographical region, and clearly less similar to all sequences from other species. DNA sequences newly obtained for this study were deposited in Genbank (accession numbers ##########<u> to be added upon manuscript acceptance</u>).

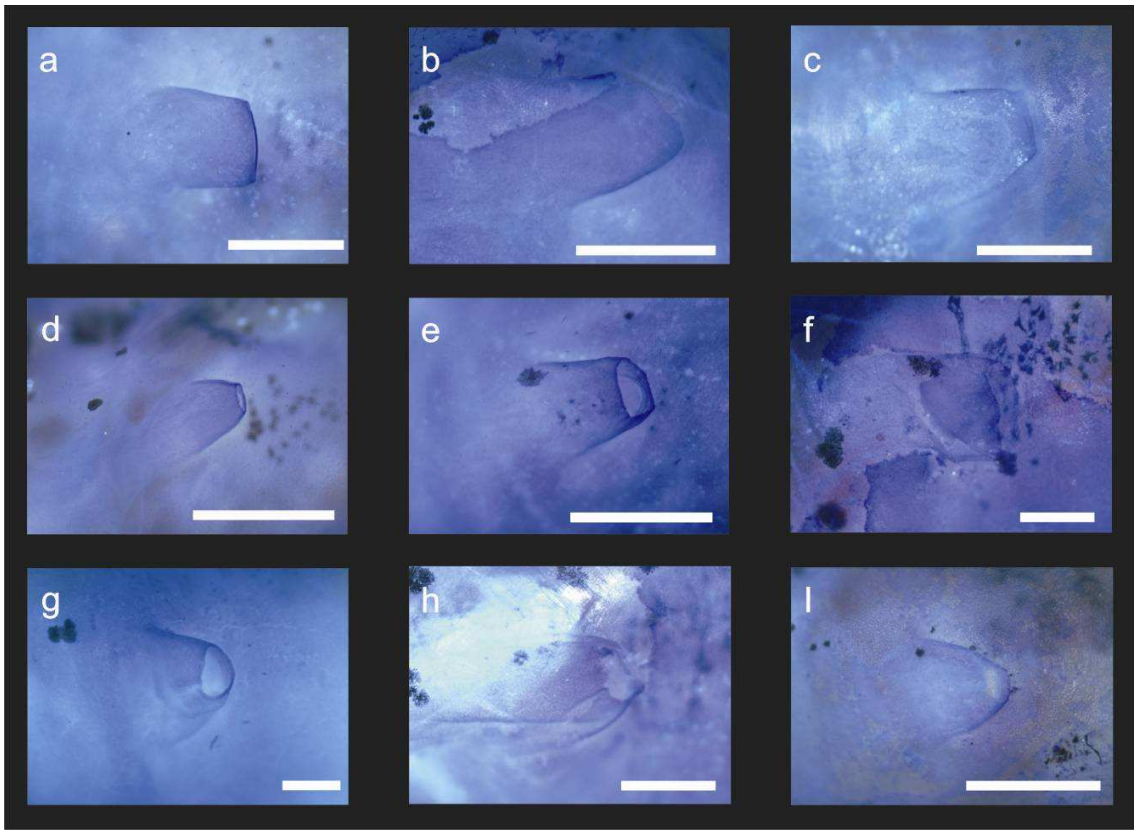

Figure 4. Photographs of the spiracle showing the opening type (stained with methylene blue). *Opening posterior*: **a** – from Fierenana (ZSM 808/2004); **b** – from Ranomena (ZSM 172/2008 - ZCMV 3807); **c** – from Belle Vue (ZSM 0608/2007 - ZCMV 5189). *Opening posterolateral*: **d** – from Fierenana (ZSM 839/2004); **e** – from Ranomena (not a voucher specimen ZSM 172/2008 - ZCMV 3807); **f** – from An'Ala (ZSM 1711/2007 - ZCMV 3406). *Opening lateral*: **g** – from Ranomafana National Park (ZSM 196/2007 - ZCMV 5050); **h** – from An'Ala (not a voucher specimen ZSM 1711/2007 - ZCMV 3406); **i** – from Ambohitsara (ZSM 77/2008 - ZCMV 4941). The scale bars represent 1 mm.

3. Ecological field data and analysis

Within a study on stream tadpole communities in the Ranomafana National Park (RNP) in the southern central east of Madagascar, species occurrence was recorded in 33 streams. To be first able to evaluate habitat features of importance for breeding stream site choice of frog species, the following habitat parameters of the streams and their surrounding forest were recorded: slope, width, depth, overhanging vegetation, and canopy cover of the stream; the density of shrubs, small trees, big trees, depth of leaf litter, slope of the forest floor, and canopy cover of the forest. Within the stream, 30 m long sections have been exhaustively sampled for tadpoles. The sampling process was separate for all available microhabitats within the section. These microhabitats were predefined subject to underground substrate (rock, gravel, leaves, sand) as well as separately by the stream velocity categories "fast" (obviously running) and "slow" (almost stagnant) resulting in eight different possible types of microhabitat. To be able to test for microhabitat preferences of the tadpoles, the frequency of the microhabitats available was recorded for each stream. Tadpoles sampling was conducted in the wet season 2008 (January and February) and repeated in a subset of 13 of the streams during the dry season (July) 2008. The dry season is assumed to be less suitable for frog reproduction in RNP than the wet season (Andreone 1996), which might be mainly caused by the low temperature from June to August.

To analyse breeding site choice of *Boophis picturatus* frogs, first a principal component analysis (PCA) was performed using on all 12 habitat parameters of all 33 streams sampled during the tadpole community study. PCA was run on the correlation matrix in order to standardise for the influence of unequal variance. To evaluate data outliers and linear interdependence of variables, box-plots and pair-plots (Zuur et al. 2007) were used. As PCA requires multinormality of data, box-cox-power-transformations (Box & Cox 1964) were applied when necessary. The significance of the PC loadings was assessed based on the bootstrapped-eigenvector method as suggested by Peres-Neto et al. (2003). The number of meaningful PCs was estimated by a screen plot (Zuur et al. 2007). A multiple logistic regression (glm with binomial error structure) with the first three PCs as independent variables and the incidence of *B. picturatus* tadpoles as binary dependent variable was run to extract the key habitat features important for breeding site choice of these species. Independent terms and interaction terms were deleted sequentially from all full models based on Akaike's Information Criterion (AIC, Burnham & Anderson 1998) until the minimum adequate models were reached. The same procedure was applied on incidence data of further groups of tadpoles to better evaluate breeding site choice of *B. picturatus*. These tadpoles belonged to two morphologically different groups of tadpoles: suctorial *Boophis* tadpoles and the funnel mouthed tadpoles of the *Mantidactylus* subgenus *Chonomantis*, as well as on a third tadpole

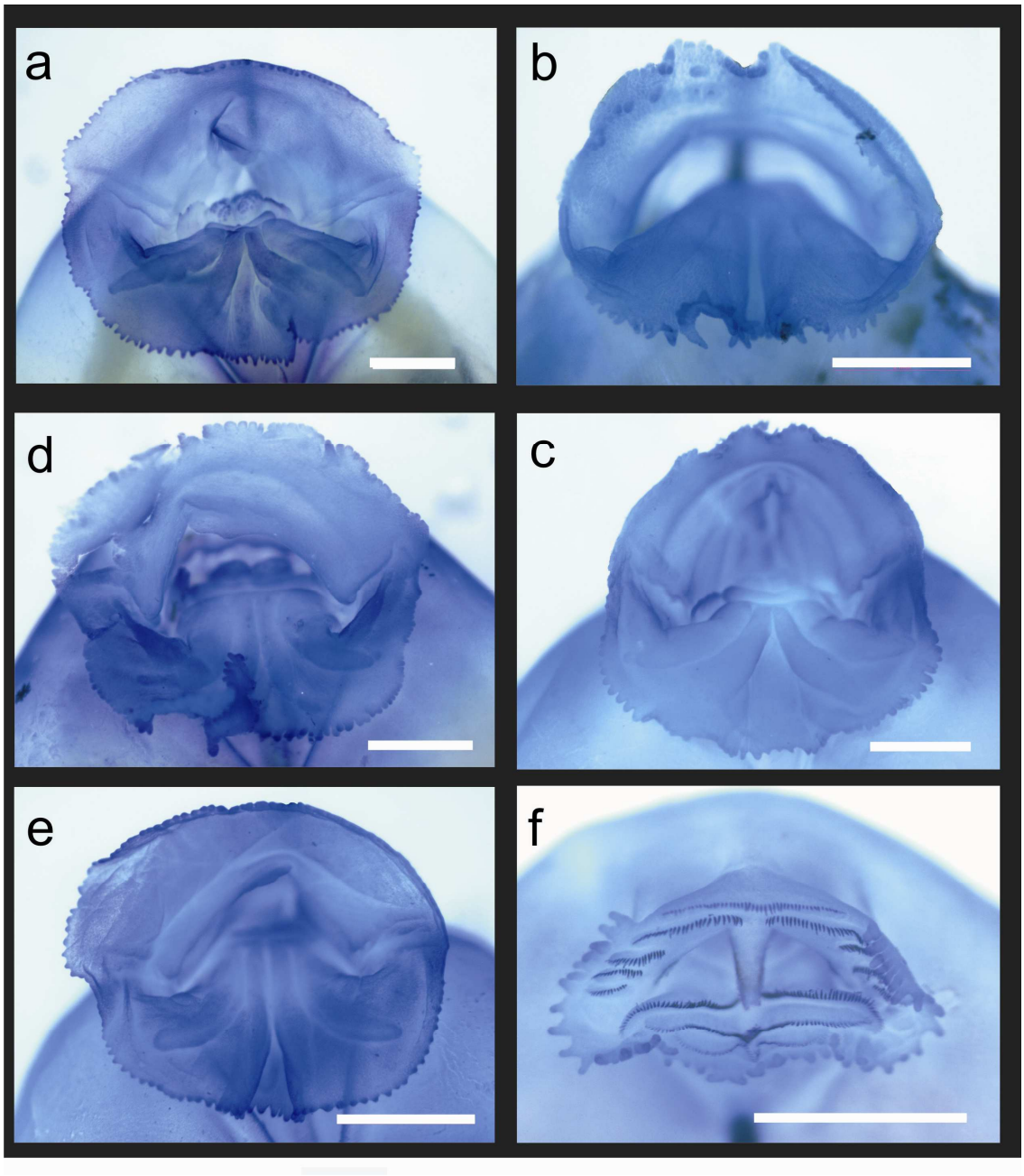

Figure 5. Photographs of the oral disc of five preserved tadpoles of *Boophis picturatus* used in this paper and one *Boophis majori* (stained with methylene blue): **a** – from Fierenana (ZSM 839/2004 - FGMV 2002.1664); **b** – from An'Ala (ZSM 1711/2007 - ZCMV 3406); **c** – from Ranomafana National Park (ZSM 196/2007- ZCMV 5050); **d** – from Ranomena (ZSM 172/2008 - ZCMV 3807); **e** – from Ambohitsara-Tsitola (ZSM 77/2008 - ZCMV 4941); **f** – *Boophis majori* from Vohiparara (ZSM 397/2008 - ZCMV 2641). The scale bars represent 1 mm.

group that similar to *B. picturatus* is characterised by strong reductions in oral disc structures: *Mantidactylus* subgenus *Ochthomantis*.

To evaluate tadpole distribution across microhabitats in the streams chosen for reproduction by this species, in a first step raw data graphing of tadpole abundance in the specific microhabitats was used. In order to quantify true preferences for microhabitats, Ivlev's electivity index (E, Ivlev 1961) was calculated. E is defined as E=(r−p)/(r+p) with r being the proportions of the microhabitats used and p the proportion of microhabitats available. The non-occurrence in an available microhabitat immediately causes a preference (avoidance) value of -1 what strongly lowers preference values even for microhabitats that were used relatively often. Therefore, only those streams were chosen for calculations in which at least 8 specimens of *B. picturatus* were found to provide the probability of having one individual in every microhabitat. One-way ANOVA was performed to test for differences in habitat use.

Results

1. Description of the tadpole

External morphology

The external morphological description is based on a DNA voucher specimen in stage 26 (ZSM 821/2004, field number FG/MV 2002/1835, BL 11.7 mm; accession number to be added upon manuscript acceptance). Because a part of the tail was removed for DNA barcoding purpose, information upon vent tube, tail fin and tip of tail was taken on another individual in stage 27 (ZSM 833/2004, TL 37.1 mm, BL 14.6 mm), as well as measurements for calculation of ratios and drawings. Another specimen in stage 25 (ZSM 808/2004, TL 18.3 mm, BL 7.7 mm) was used for the drawing of the oral disc because it was the less closed of all specimens in hand. Raw measurements of six DNA voucher *B. picturatus* tadpoles from different localities are provided in Appendix 3,Table 4, 5, and 6.

In dorsal view (Figure 1a), body elliptical, widest in the middle of coiled intestine, snout nearly rounded. In profile, (Figure 1b), body depressed, BW 138% of BH, snout rounded. Eyes moderately large, ED 14% of BL, bulging, not visible in ventral view, positioned more dorsally than strictly dorsolaterally and directed slightly more laterally than strictly dorsolaterally and anterolaterally. Nares elliptical, large, rimmed with a very slight posteromedial projection, positioned almost dorsally and directed slightly more laterally than strictly anterolaterally and more dorsally than dorsolaterally, closer to snout than to pupils RN 90% of NP; NN 63% of PP.

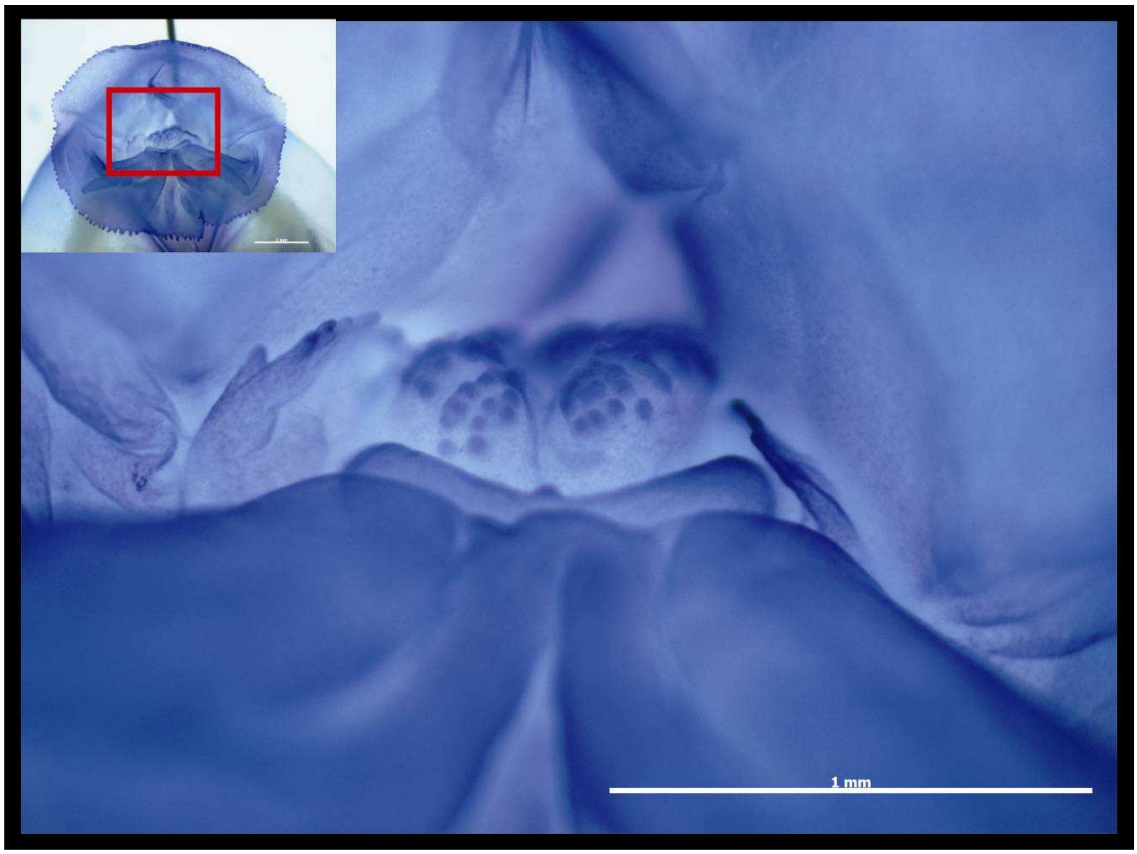

Figure 6. Photographs of the oral disc of the tadpole of *Boophis picturatus* (ZSM 808/2004 - FGMV 2002.1664) stained with methylene blue, showing the densely packed pustular protuberances of the prelingual arena.

Spiracle sinistral, slightly conical, small, attached to body wall but its tip free, laterally positioned, oriented posteriorly, slightly closer to end of body than to tip of snout, SS 67% of BL; spiracular opening at the height of the apex of caudal myotomes. Tail musculature moderate, TMH 66% of BH and 65% of MTH, TMW 46% BW, gradually tapering, almost reaching tail tip. Upper tail fin of moderate size, UF 32% of MTH, not extending onto body, SU 89% of BL, beginning at the dorsal junction of caudal muscle and body, slightly convex though it increases abruptly at the proximal sixth; lower fin moderately shallow, LF 19% of MTH, following the caudal muscle; point of maximum height of tail located just before halfway of tail, MTH 101% of BH, tail tip irregularly rounded. Coiled gut very short (three loops) filled with sand and sediments. Anal tube moderately large, dextral to ventral fin, like a large tube, directed posteriorly, linked to ventral tail fin except the tip, opening dextral, bevelled, directed posterodorsally. No lateral line organs nor glands visible.

Oral disc (Figure 1c) positioned ventrally, directed posteriorly and slightly ventrally, not emarginated, of moderate size, ODW 30% of BL and 52% of BW. Upper labium bowl-shaped, slightly concave, covering most part of the mouth opening at rest. Lower labium projecting anteroventrally, the medial part folded longitudinally on a small space forming up a depression in which lies a straight low-profile ridge on most of the length of the labium; two other pairs of such ridges lie laterally to the medial one, these ridges curved towards the sides of the lower labium. An uninterrupted row of small and round marginal papillae around the oral disc. No submarginal papillae. No denticulate papillae. No keratodonts. Upper jaw sheath shallow, convex medially, bearing no serrations and not keratinized; lower jaw sheath as a short rectangle, slightly concave, ending abruptly laterally, bearing no serrations and very few keratinized.

Colour in preservative: Tegument transparent, stuck out from all underlying organs laterally and anteriorly to the coiled gut. Upper side (coiled gut, extension of caudal muscle on the back, areas between the eyes, between the nares and anteriorly to them) coloured by densely arranged dark brown dots contained in underlying tissues. Two unpigmented areas just anterior to the dorsal junction between tail and body. Upper part of flanks very few pigmented with very small dots; lower part of flanks immaculate. Ventral side immaculate and transparent, the coiled gut, the pericardium, the gills and the hyoidians muscles being very clearly visible. Anterior half of the upper part of caudal muscle densely covered with relatively large dark brown dots, as well as the anterior half of the lower part except the ventral part immaculate making some very clear white spots; posterior half with the same pattern but the density and size of the dots decrease quickly. Upper fin with some dots in the anterior third, the rest almost devoid of pigmentation, lower fin immaculate.

Variations: TL and BL of 10 other tadpoles at stage 25–37 from the batches ZSM 808/2004 and ZSM 833/2004 are respectively 22.2–39.3 mm and 8.2–14.1 mm. The ratios vary

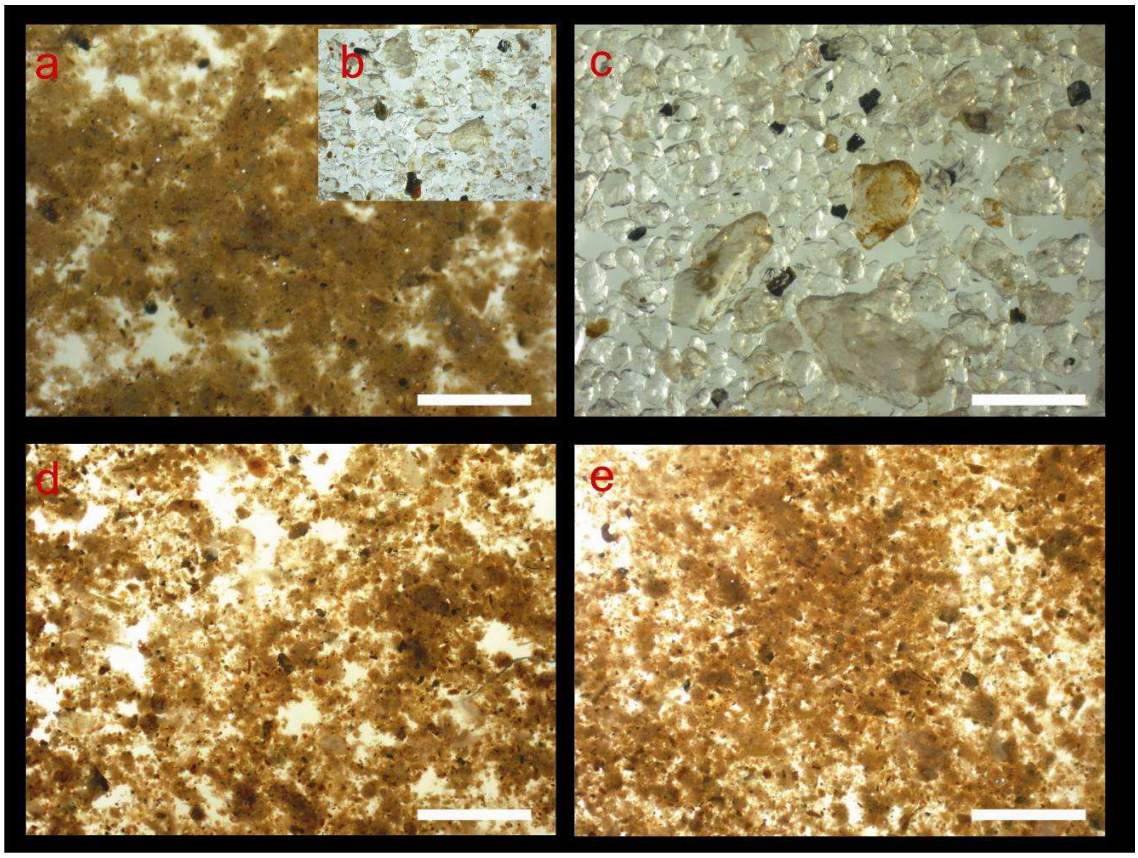

Figure 7. Photographs of the gut content of the tadpole of *Boophis picturatus* (ZSM 172/2008 - ZCMV 3807) and *Boophis majori* (ZSM 953/2008 - ZCMV 5398): **a** – Organic material in the front part of *B. picturatus* intestine; **b** – Sand grains in the front part of *B. picturatus* intestine; **c** – Sand grains in the rear part of *B. picturatus* intestine; **d** – organic material in the front part of *B. majori* intestine; **e** – organic material in the rear part of *B. majori* intestine. The scale bars represent 1 mm.

in the following proportions: BW 119–135% of BH; ED 14–18% of BL; RN 64–106% of NP; NN 50–62% of PP; SS 49–57% of BL; TMH 48–63% of BH; TMH 46–60% of MTH; TMW 37–54% of BW; UF 36–41% of MTH; SU 79–108% of BL; LF 21–31% of MTH; MTH 97–117% of BH; ODW 25–35% of BL; ODW 38–51% of BW.

Eight other tadpoles at stage 25 from the batch ZSM 808/2004 have an average TL 15.9 ± 2.5 mm (12.3–18.7, n = 5) and an average BL 6.0 ± 1.3 mm (4.4–7.2, n = 8).

The naris can also be at equal distance from snout to pupil or closer to snout than to pupil (RN/NP 64–116%). The spiracular opening can be at equal distance from snout to body terminus. The caudal spots are less numerous on certain specimens and the dots on the caudal muscle can reach the tip of the tail.

Buccopharyngeal anatomy

The description of the buccal features is based on a specimen from the batch ZSM 808/2004 at stage 25 (BL 5.4 mm).

Buccal floor (Figure 2a). – Buccal floor trapezoid, as large as long. Prelingual arena as a longitudinal slit surrounded by numerous densely arranged protuberances pustulate at top (composed of tightly spaced elements as protuberances of different sizes, flaps and even papillae which could be an agglomeration of papillae of the same kind than the pustulate buccal floor arena papillae); these protuberances form a truncated triangle whose tip is anterior, the largest anterior; at the posterior end of the arena lies a pair of flaps with a jagged and pustular edge, the infralabial papillae, directed posterodorsally. Tongue anlage hidden in a cavity, seemingly very narrow and elongate bearing a pair of small lingual papillae. Buccal floor arena trapezoid, delimited by less than one hundred of tightly spaced buccal floor arena papillae whose the most anterior lie lateral to the tongue anlage and the most posterior are near the free end of the ventral velum; the external buccal floor arena papillae are the biggest (especially those in front of the buccal pockets), certain bifide, but always smooth, then their size decreases toward the centre of the arena with their tip becoming pustulate. The interior of the arena is occupied anteriorly by these smaller pustulate papillae, and the centre and the posterior parts are occupied by large and very densely arranged pustules forming a pustulate longitudinal ridge. Buccal pockets straight, fine, slightly oblique, not perforated, closer to tongue anlage than to medial end of the ventral velum; prepocket papillae mixed with the buccal floor arena papillae and not distinct from them. Ventral velum with spicular support, slightly waving, bearing no projection, a very deep median notch of about 20% of the buccal floor length, reaching the medial longitudinal pustulate ridge and bearing a pustulate flap on one side; secretory pits not visible. Glottis not observed (damaged during dissection?). Branchial baskets not observed.

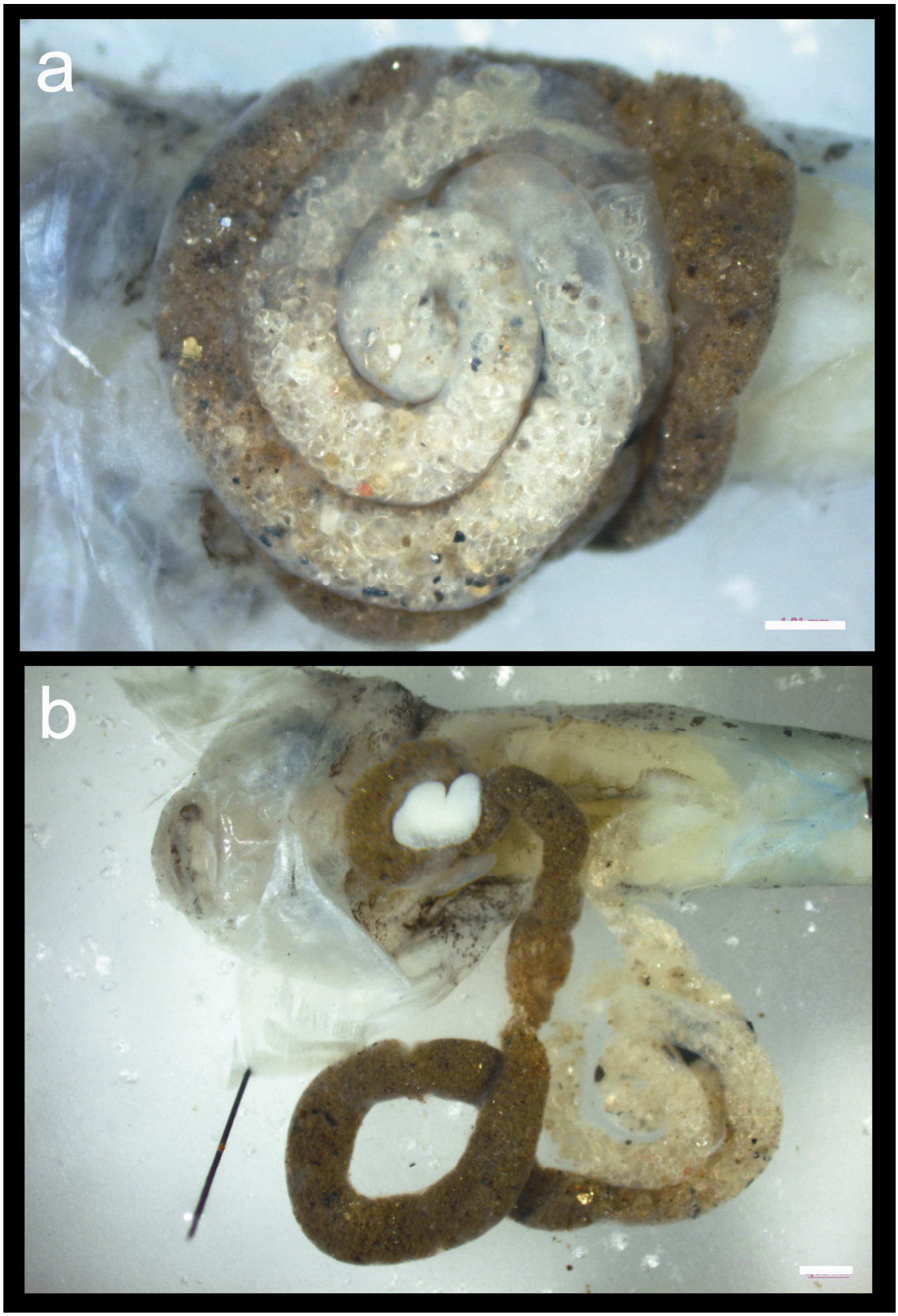

Figure 8. Photographs of the gut of the tadpole of *Boophis picturatus* (ZSM 172/2008 - ZCMV 3807) showing the difference state in the front and the rear part: **a** – coiled; **b** – uncoiled. The scale bars represent 1 mm.

Buccal roof (Figure 2b). – Prenarial arena trapezoid; prenarial ridge missing or limited to a pair of small and smooth protuberances anterolateral against the anterior wall of the arena; interior smooth with only a few tiny pustules. Choanae fines, slightly anteromedially oriented; anterior wall bearing a fine prenarial papilla on its external half oriented posteromedially above the opening, the edge of the anterior wall pustulate; narial valve smooth except the tip pustulate, barely bigger than the anterior wall. Postnarial arena with eight pustules of different forms and not uniformly arranged; a bunch of long and fine, sometimes bifid papillae (probably homologous to postnarial papillae) of the same type than the buccal floor and roof arena papillae. Median ridge triangular, low and pustulate on its free edge and on its posterior side. Lateral ridge papillae absent. Buccal roof arena round, delimited by 25–30 buccal roof arena papillae on each side of the same type than the buccal floor arena papillae, oriented roughly medially; interior of the arena covered with large pustules close together. Posterolateral ridges absent. Glandular zone not observed. Dorsal velum damaged during dissection.

2. Genetic variation in *Boophis picturatus*

The available DNA sequences, all of the mitochondrial 16S rRNA gene, fell into two major groups which were separated among each other by 3.0-3.9% uncorrected sequence divergences. The first of these clades contained samples from the Ranomafana area, including the Ambohitsara forest, and from Vevembe, in the southern central east of Madagascar. The second clade contained samples from An'Ala and Fierenana in the northern central east. Within the two clades, samples were very uniform, with divergences of 0-0.5%, and with identical haplotypes shared by the populations of Ambohitsara and Ranomafana within first clade and by Ambohitsara and Ranomafana in the second clade. The single available sequence from Vevembe was also very similar to those from Ranomafana, differing by only 0.3-0.7%.

3. Variability of external morphology of *B. picturatus* tadpoles from different localities

In life, all *Boophis picturatus* have the same coloration and pattern, generally yellowish brown (see example T 08/0076 in comparison to *B. majori* ZSM 37/2007 - ZCMV 1369; Figure 3). Yellowish brown area positioned in layers deeper than the skin covered the dorsum and the upper part of the flank. Dark brown blotches spread irregularly and condensed over the brain and on the dorsal part of the tail muscle. Silvery patches spread over the skin, mainly on the dorsum. Ventrally, oral disc and gular regions are transparent, the branchial region is reddish making the

Figure 9. Clutch of *Boophis picturatus* from a site named Fompohonina III. From the clutch that was attached on a twig under water, few eggs were sampled and identified by DNA barcoding (field number ZCMV 9849).

beating heart and gills visible. The abdominal surface is translucent with few silvery patches and intestinal coils are well visible with a regular spiral shaped intestine. Tail musculature is transparent with yellowish zone and scarce light brown dots consolidated forming patches. Fins are transparent. The dorsal fin is patched and the ventral fin is free of pigments. The lateral space under the skin is well visible. In preservative, tadpoles loose the silvery iridiophoric pigment; only the brown melanophoric pigments are left.

The observation of preserved *Boophis picturatus* tadpoles from Ranomafana National Park, An'Ala, Ranomena, and Ambohitsara-Tsitolaka shows the typical morphology of the species making it easily to distinguish them from *B. majori* (ZSM 397/2008 - ZCMV 2641) tadpoles (Appendix 3 - Table 6). They are all characterized by the transparency of their integument letting most of their organs clearly visible. Their large nares are situated at about halfway between snout and eyes or closer to snout, but they are always closer to the snout in *B. majori*. They have also a large vent tube in comparison with *B. majori* (Appendix 3 - Table 5). Only the tadpole from Ambohitsara-Tsitola appears to differ by having a smaller spiracle than the others. A variation in the configuration of the opening of the spiracle in many tadpoles (ZSM 808/2004, ZSM 0608/2007 - ZCMV 5189, ZSM 839/2004, ZSM 172/2008 - ZCMV 3807, ZSM 1711/2007 - ZCMV 3406, ZSM 196/2007 - ZCMV 5050, ZSM 77/2008 - ZCMV 4941) was observed (Figure 4). Tadpoles from Fierenana, Ranomena and some of Ranomafana National Park were found having an inner wall free from body and an aperture opening posteriorly; some tadpoles from Ranomafana National Park and of An'Ala, and those Ambohitsara also have an inner wall free from body but with an aperture opening laterally instead of posteriorly and an intermediate configuration was discovered in tadpoles from Fierenana, Ranomena and some of An'Ala (Figure 4e-g).

All observed *B. picturatus* tadpoles (ZSM 839/2004-FGMV 2002.1664, ZSM 1711/2007 - ZCMV 3406, ZSM 196/2007 - ZCMV 5050, ZSM 172/2008 - ZCMV 3807, ZSM 77/2008 - ZCMV 4941) have a large, ventral, and non emarginated oral disc with complicated folds in the lower labium and lacking all the typical keratinized components of generalized oral disc (Appendix 3 - Table 6; Figure 5). Opening the oral disc maximally allows seeing a characteristic structure with the densely packed pustular protuberances of the prelingual arena (Figure 6).

4. Gut content analysis

Three non voucher tadpoles of *B. picturatus* (ZCMV 4017 - ZSM 680/2007) from Ranomafana National Park and one *B. majori* (ZCMV 5398 - ZSM 953/2007) from Ranomena were dissected for the gut content observation (Figure 7). *B. picturatus* tadpoles have a rather short

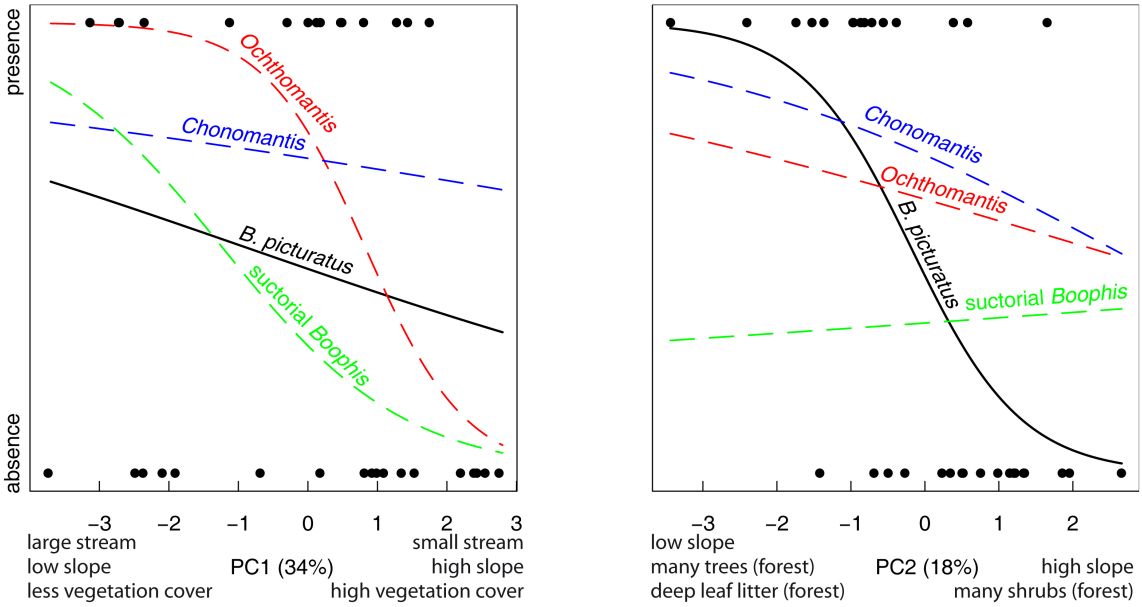

Figure 10. Breeding site choice of *Boophis picturatus* represented by incidence of tadpoles in streams of RNP along the PC1 and PC2 gradient. Each symbol represents a stream; the regression line of the logistic regression is plotted as black line. For comparison, the logistic regressions of three other abundant tadpole groups are overplotted.

intestine in comparison with *B. majori* (a mean of 100 mm *vs.* 144 mm; Table 1). The whole intestine of *Boophis picturatus* is full of grains of sand, but the front part contains also organic materials (Figure 8). External observation of all the living *B. picturatus* tadpoles that we captured in Ranomafana National Park in 2006 and 2007 reveals a similar situation.The analysis of the sand grains in the *B. picturatus* intestine shows a size range from 0.1 to 1.4 mm (Table 2). The general observation indicates rather higher number of sand grains in the rear part except in the size range <0.2 mm. The majority of sand grains were between 0.2–0.4 mm, and those bigger than 1 mm were rare. As shown in Fig. 8a, in natural condition the rear part of the intestines is exposed ventrally, showing many sand grains under the skin which suggests a low quantity or even an absence of organic material in the rear part after the digestion process. On the other hand, the whole intestine *B. majori* tadpoles is full of organic materials, with many small sand grains <0.2 mm but no prevalence of large sand grains (Table 2), and the rear part of the gut is not "cleaned" after digestion process (Figure 7d).

5. Ecology

During the wet season 2008, 33 streams in RNP were sampled for tadpoles. In 15 of these streams, the specialised tadpoles of *Boophis picturatus* have been found. Compared to other species in that area (Grosjean et al. 2011; Randrianiaina et al. 2011), tadpoles of this species are moderately abundant. There were 193 specimens in 15 out of the 33 stream (minimum 1, maximum 35, mean of 13 specimens per stream). The same is true for the dry season, in which in 6 out of 13 sampled streams the number of 56 tadpoles varied from 1 to 23 specimens per stream with a mean of 9. If *B. picturatus* tadpoles have been observed in a stream in the dry season, in the same stream tadpoles of these species were also sampled in the wet season. Also, the streams without these tadpoles in the dry season did also not harbour them in the wet season. Additionally, clutches of eggs of this species were found at two streams. One clutch was attached on a twig under water surface, consisting of about 50 eggs (Figure 9). Another clutch was attached on a broken stick lying on a rock just above water surface.

To ordinate habitat characteristics of the streams available to *B. picturatus*, PCA on the habitat variables of the stream and the surrounding forest was performed and resulted in three principal components, explaining together 67.6% of the variation in the data. Based on the loadings of the PC and the results of the bootstrapped-eigenvector method (Peres-Neto et al. 2003) we identified the following habitat variables being well represented: PC1 (33.9%) positive: slope and canopy cover of forest and stream, overhanging vegetation; negative: width and depth of the stream. The strongest contributors to PC2 (18%) were positive: slope of the stream and the

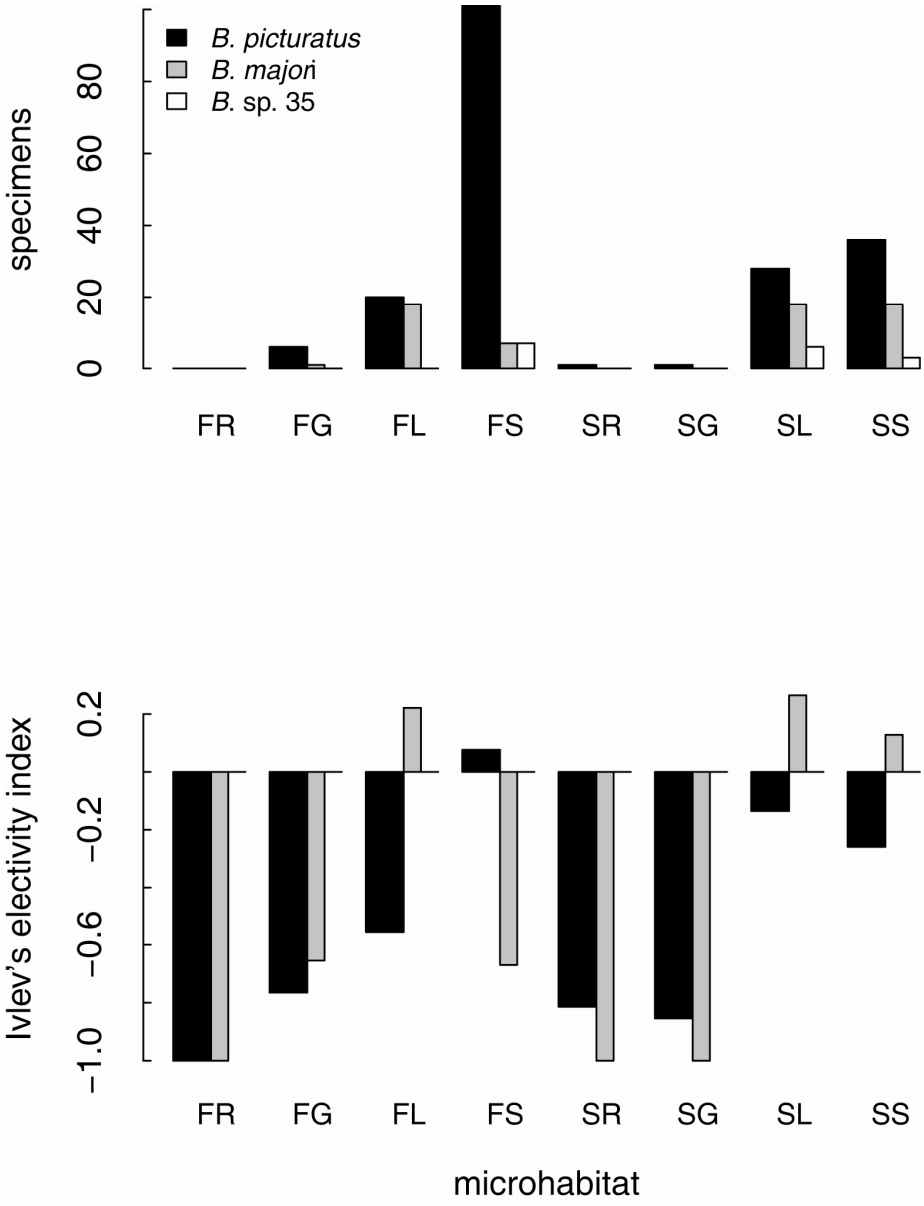

Figure 11. Distribution of *B. picturatus* tadpoles across eight microhabitats in the streams of RNP and distribution of *B. majori* and *B.* sp. 35 tadpoles for comparison. Given are (upper graph) the absolute abundance values from all observations (N=15 streams) during the wet season 2008 and (lower graph) calculated preferences / avoidance for the microhabitat, taking microhabitat availability into account and using Ivlev's electivity index (E, Ivlev 1961). For the latter, only streams with at least 8 *B. picturatus* specimens (N=10 streams) were used. For *B.* sp. 35, no electivity index was calculated.

number of shrubs in the forest; negative: number of trees and leaf litter depth, to PC3 (15.7%) were positive: number of small trees and shrubs in the forest and overhanging vegetation.

Using a multiple logistic regression with backward selection, PC1 and PC3 were identified as not being of importance for breeding site choice (=presence of tadpoles) of *B. picturatus* frogs, as both terms were deleted from the model (Figure 10a). PC2 remained as factor of highly significant importance for breeding site choice (multiple logistic regression with binomial error structure; residual deviance: 31.3 on 31 d.f., $p<0.004$; Figure 10b). As PC2 was negatively correlated with *B. picturatus* tadpole incidence, this species prefers streams with a low slope in forest areas with high number of trees but less shrubs and thick leaf litter.

Within the streams they occurred, *B. picturatus* tadpoles were unequally distributed across all microhabitats (Figure 11a). By far most of the specimens were found above sandy substrate, mainly in non-stagnant parts of the stream. Also microhabitats with accumulations of dead leaves harboured *B. picturatus* tadpoles, almost none were found above stony substrates (rock, gravel). A true preference or avoidance can only be evaluated taking the availability of different microhabitats into account: there was no positive preference for any kind of microhabitat. ANOVA revealed that even the fast sand habitat was not used more than expected by a random distribution across all microhabitats (ANOVA, $F_{7,56}=4.2$, $p_{model}<0.001$, $p_{FastSand}=0.65$). However, for interpretation it needs to be noticed that fast sand is by far the most available habitat. The same is true for slow leaves ($p_{SlowLeaves}=0.42$) and slow sand microhabitat ($p_{SlowSand}=0.13$). All other microhabitats were used by this species significantly less often that expected by a random distribution among microhabitats (all $p<0.002$).

Discussion

1. Morphological comparisons

The tadpole of *Boophis picturatus* shows a very derived and peculiar oral morphology among Mantellidae that is also unique compared to other anuran larvae. It is devoid of keratinized structures (jaw sheaths and keratotodonts) and has unique labia, especially the lower one which is a flap of skin bearing radiating longitudinal low ridges, and which folds medially at rest. Most other *Boophis* have rather generalized oral morphologies with keratinized jaw sheaths and keratodonts present and specializations mainly on the axis towards a suctorial oral disc with increased numbers of keratodont rows and labial papillae (*e.g.*, Blommers-Schlösser 1979; Raharivololoniaina et al. 2006; and Randrianiaina et al. 2009a, b). Although a trend towards reduction of keratinized structures is apparent in *B. majori* and *B.* sp. 35 (as *B.* sp. aff. *majori*)

Table 1. Characteristics of tadpoles in which gut content are observed

ZSM	Species	Stage	BL (mm)	TL (mm)	Intestine length (mm)
680/2007	*B. picturatus*	27	12.9	22.0	110.0
680/2007	*B. picturatus*	26	13.6	23.2	106.5
172/2008	*B. picturatus*	27	14.5	23.3	89.6
953/2007	*B. majori*	27	10.5	16.2	144.3

Table 2. Gut content result showing the number of sand grains by size classes recovered from the intestines of *Boophis picturatus* and *Boophis majori* tadpoles for each of the three square plots.

Sand diameter	< 0.2 mm	0.2 - 0.4 mm	0.4 - 0.6 mm	0.6 - 0.8 mm	0.8 - 1 mm	> 1 mm
ZSM 680/2007 (stage 27)	14	51	10	2	-	-
(front)	17	52	11	1	-	-
	13	73	8	2	-	-
ZSM 680/2007 (stage 26)	13	94	29	4	-	-
(front)	6	95	29	3	-	-
	5	69	21	3	3	1
ZSM 953/2007 (stage 27) (front)	many	-	-	-	-	-
ZSM 680/2007 (stage 27)	10	95	20	3	-	-
(rear)	6	85	26	3	1	-
	7	76	20	5	1	-
ZSM 680/2007 (stage 26)	3	40	24	3	3	-
(rear)	17	52	20	7	3	2
	6	73	23	6	3	1
ZSM 953/2007 (stage 27) (rear)	many	-	-	-	-	-

(Schmidt et al. 2008), the tadpole of *B. picturatus* is to date the only tadpole in the mantellid subfamily Boophinae totally devoid of such structures.

Altig & McDiarmid (2006) described the external morphology of the tadpole of *Boophis picturatus* and gave brief information about its buccopharyngeal anatomy. The identification of the species was based on our molecular data that we provided to the authors, and on the fact that our specimens had the same unique morphology and were collected from the same general area (Ranomafana). Not unexpectedly, thus, our description matches in all aspects the one published by Altig & McDiarmid (2006), except that we found the lower jaw being very slightly keratinized. Even if the tadpole drawn by Altig & McDiarmid seems more elongate, the proportions of their and our specimens fit. For example, the ratio BL/TL is 37% in the Altig & McDiarmid's description and 34–41% in ours, and the ratio BW/BH is 119–141% in our specimens and 140% in the previous description though it is considered as "slightly depressed". The colour pattern and the buccopharyngeal features described by Altig & McDiarmid (2006) matches also very well with those of our specimens. Nevertheless, these authors described "Two large lingual papillae with large, clavate, papillate heads (...) arranged transversely on the oval tongue anlage and bordered posteriorly by four smaller but similarly structured papillae". These structures are indeed present in the buccal floor of our dissected specimen but we rather interpret them as posterior infralabial papillae due to their position relative to the lower jaw. The tongue anlage, although not very clearly visible seems to lie in a depression, be very narrow, and bear a pair of small simple and smooth lingual papillae.

Tadpoles of the genus *Boophis* are mostly pond to stream dwellers with classic adaptations to these habitats such as a very depressed body, low caudal fins, large oral disc with numerous keratodont rows and multiple rows of tightly spaced small marginal papillae for the torrent dwellers for example (Raharivololoniaina et al. 2006; Randrianiaina et al. 2009b). Whereas species of another large mantellid genus, *Mantidactylus*, show a very high ecomorphological diversity of tadpoles, very few cases of divergence from this pattern are known among the members of the genus *Boophis*. Besides *B. picturatus*, only two tadpoles show derived oral disc structures, *B. majori* and *B.* sp. 35 (Glaw & Vences 2007; Schmidt et al. 2008). Very interestingly, molecular analyses suggest that these three species belong to the same clade (Vieites et al. 2009). These results indicate that the tadpoles of this lineage (rather than the adult forms) are derived and that their evolutionary history took a different way than the other members in the genus *Boophis*. Although the tadpoles of *B. majori* and *Boophis* sp. 35 possess derived oral structures (much more derived in the first species than in the second), these evolved in the same way, are very different than that of *B. picturatus* and so are unique to these two species. The most remarkable characters are the presence of a strong medial convexity on the upper jaw sheath (particularly long and narrow in *B. majori*), the presence of a few large marginal and submarginal

papillae directed in a radial pattern and the folding of the lower labium at rest. Furthermore, the tadpole of *B. majori* has an interrupted upper keratodont row on the upper labium which is extremely rare in the anurans larvae. The rest of the morphology of these two species is on the other hand "classic" (note that certain ratios given for the tadpole of *B. majori* by Schmidt et al. [2008] seem to be wrong, such as BW 84% of BH or ED 29.3% of BL).

The unique tadpole of *B. picturatus* fits none of the ecomorphological guilds proposed by Altig & Johnston (1989). It is exotrophic and lotic, but cannot be assigned to any of the lotic categories. The closest guilds are *(1)* the "psammonic" guild defined for the tadpole of *Otophryne robusta* which lives buried in sand but feeds on microorganisms living in sand by passive filtering, has no keratodonts but possesses hypertrophied serrations on the jaw sheaths (Wassersug & Pyburn 1987), and *(2)* the "psammonektonic" guild which was recently defined for the lentic tadpoles of the genus *Scaphiophryne* (Mercurio & Andreone 2006) which possess keratinized jaw sheaths but no keratodonts and which absorb sand particles and detritus during day with half the body buried in sand and the body and tail axis at 35–40°, and swim through the water column in filtering suspended particles at night. Hence, the tadpole of *B. picturatus* probably deserves the creation of a new guild within the exotrophic lotic group. On the contrary, tadpoles of *B. majori* and *Boophis* sp. 35 likely belong to the "lotic clasping" guild of Altig & Johnston (1989).

The clade containing *B. majori*, *Boophis* sp. 35 and *B. picturatus* also contains *B. miniatus*, *B. feonnyala* and further undescribed species whose tadpoles are not known at present. The knowledge of the morphology of the tadpoles of these species and especially of their oral specializations will certainly shed light on the evolutionary tendency of the ecology and morphology of the tadpoles of this lineage.

2. Ecological comparisons

Although the oral morphology is greatly different between *B. majori* and *Boophis* sp. 35 on the one hand and *B. picturatus* on the other hand, these three species are closely related (Vieites et al. 2009), live in the same kind of habitat (slow running streams with a sandy substrate) and from preliminary observation of their gut content they seem to absorb the sand particles for feeding (Altig & McDiarmid 2006; Schmidt et al. 2008; this paper) though in different proportions. The comparisons of the gut content of *B. picturatus* and *B. majori* shows a difference by the presence of many big sand grains in *B. picturatus*. *B. majori* has many small sand grains (< 20 mm) and the maximal size is up to 0.5 mm. This indicates a higher trophic specialization in *B. picturatus*, in accordance with its more specialized oral morphology.

In the tropical rainforest of Ranomafana National Park, the tadpoles of *Boophis picturatus* occur throughout the whole year with clearly higher abundances in the wet season. The same has also been observed for other species in this region (*e.g.*, Randrianiaina et al. 2011, R. D. Randrianiaina unpublished data). Compared to these and other species from the RNP region, *B. picturatus* tadpoles occur with moderately high abundance in a moderately high number of streams. Interestingly, streams typically harbouring *B. picturatus* tadpoles are characterised by different habitat variables of the stream and the surrounding forest than the ones often used by other prominent groups (Figure 12). The morphologically very different suctorial *Boophis* tadpoles and the less closely related tadpoles of the *Mantidactylus* subgenus *Ochthomantis*, which are characterised by a strong reduction of oral disc structures comparable to *B. picturatus* both, depend on PC1 but not PC2 (Randrianiaina et al. 2011). All three groups therefore choose streams with low slope and therefore low water current, the main difference is that trees and leaf litter seem to be important for *B. picturatus* whereas it is more the size of the stream that is important for the two other groups. The adults of a fourth group, the *Mantidactylus* subgenus *Chonomantis* with specialised funnel-mouthed tadpoles, do not choose their breeding habitat comparable to the other three groups, as for some species no prediction of occurrence by habitat characteristics is possible and some species (*e.g.*, *Mantidactylus opiparis*) prefer combinations of habitat characteristics that are unfavourably represented in our PCs (Grosjean et al. 2011). Comparable analyses of breeding site choice of the closest relatives of *B. picturatus*, *B. majori* and *B.* sp. 35 (Vieites et al. 2009) in RNP are difficult due to their rareness in the streams studied (found in four and two streams, respectively). They were always recorded from streams where also *B. picturatus* tadpoles were found and as far as it is reasonable to state for *B. majori*, their occurrence turned out to be not depending on PC1 but on PC2, as observed for *B. picturatus* (own unpublished data).

B. picturatus uses the same streams for reproduction throughout the year, and (based on a single observation) clutches are attached on structures like sticks in the water (Figure 9). The second clutch observed attached to a stick lying on a rock was most likely washed there by the water current.

Within the streams, by far most of the *B. picturatus* tadpoles recorded occur in patches with sandy substrate, preferably where water is non-stagnant (Figure 11a). The concentration in this microhabitat differs from the pattern observed in other tadpoles in streams in RNP (see also Altig & McDiarmid 2006), especially because most other species are very often found in leaf accumulations (Grosjean et al. 2011; Randrianiaina et al. 2011), or also use stony parts of the streams (R. D. Randrianiaina unpublished data). Also tadpoles of *B. majori* and *B.* sp. 35, which show markedly lower abundances, do not share this clear distribution across microhabitats (Fig.

11) although they also have derived oral disc structures and were observed to have ingested sand particles (Schmidt et al. 2008, this study). The dominant use of this kind of microhabitat is obviously related to very specific feeding type of *B. picturatus* tadpoles, given that also their colouration in life makes them cryptic on sandy background (Altig & McDiarmid 2006). Altig & McDiarmid (2006) stated that sand grain size may be of importance for these tadpoles, a possible explanation for finding most tadpoles in fast sand microhabitat where sand grains are bigger than in the slow-moving or almost stagnant parts of streams. This correlation is supported by the fact that both *B. majori* and *B.* sp. 35, which are most likely found in leaf accumulations or slow moving sandy parts of the stream, have sand particles of smaller size in their guts. A number of *B. picturatus* tadpoles were also found where leaves accumulated in the stream. They obviously do not use this microhabitat for feeding (Altig & McDiarmid 2006), and also protection from predators seems unlikely as there are no fish in these streams and dragonfly larvae as well as larger crustaceans, both the potential main tadpole predators in these streams (own unpublished data), can enter leaf accumulations.

However, relating pure abundance data with microhabitat availability does not reveal true preferences for sandy habitat; since "fast sand", "slow sand", and also "slow leaves" were used as much as expected by a random distribution of *B. picturatus* tadpoles among all microhabitats. For an interpretation of these findings it needs to be noticed that firstly, fast sand is by far the most available microhabitat in these streams, and secondly, the calculation of preferences can only be done using relative abundance within a stream. Whereas most specimens of *B. picturatus* were found in "fast sand" the percentage of specimens within each stream that used this microhabitat was similar to the percentage of availability of this microhabitat. Clear instead is the strong avoidance of stony areas. This is also the case for many other species that have no clear adaptations enabling them to attach to this kind of surface, especially in strong current (R.D. Randrianiaina unpublished data).

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Chapter 4

Diversity, external morphology and "reverse taxonomy" in the specialized tadpoles of Malagasy river bank frogs of the subgenus *Ochthomantis* (genus *Mantidactylus*)

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Abstract

We provide detailed morphological descriptions of the tadpoles of Malagasy river bank frogs of the subgenera *Ochthomantis* and *Maitsomantis* (genus *Mantidactylus*, family Mantellidae), and data on relative abundance and habitat preferences of *Ochthomantis* species from Ranomafana National Park in southeastern Madagascar. Our study includes the tadpoles of six described and four undescribed candidate species. Eight of these larvae were previously unknown. Tadpoles were identified by DNA barcoding. Due to the very rudimentary taxonomic knowledge on *Ochthomantis*, we followed a 'reverse taxonomy' approach in which adult classification was to a great part determined on the basis of larval differences. By this procedure we even identified one candidate species whose adults remain still unknown. The majority of tadpoles in *Ochthomantis* and *Maitsomantis* have a rather similar body shape and they usually have similar habitat requirements. However, on the basis of the structure of their oral disk we identified three distinct groups: the first includes the *femoralis*-like tadpoles of *Mantidactylus femoralis*, *M. ambreensis*, *M. zolitschka*, *M argenteus*, and of the candidate species named M. sp. 42, M. sp. 43 and M. sp. 47. They all have a reduced oral disk with poorly keratinized jaw sheaths and labial teeth. The *mocquardi*-like tadpoles of *M. mocquardi* and M. sp. 64 are placed in the second group and are characterized by a further reduction of oral disk structures, *i.e.*, a complete lack of labial teeth. The third group includes only *M. majori* and is characterized by the transformation of the upper jaw sheath into three thorn-shaped projections. Based on a preliminary molecular phylogenetic analysis the reduction of keratinized oral structures in *M. majori* may have occurred convergently to that in *M. mocquardi*. The ecological data indicate that the tadpoles of the three most abundant species in Ranomafana (*M. femoralis*, *M. majori* and M. sp. 47) do not obviously differ in their choice of microhabitat although the differences in their oral structures indicate that they might use different food resources. They all show a preference for the stream areas with slow current and leaf litter substrate.

Key words: Amphibia, Mantellidae, Madagascar, tadpole morphology, DNA barcoding.

Introduction

In the Malagasy family Mantellidae, frogs of the genus *Mantidactylus* form one of the most diverse groups especially in terms of their larval morphology. While the phylogenetic relationships among the various subclades (subgenera and species groups) of *Mantidactylus* are relatively well

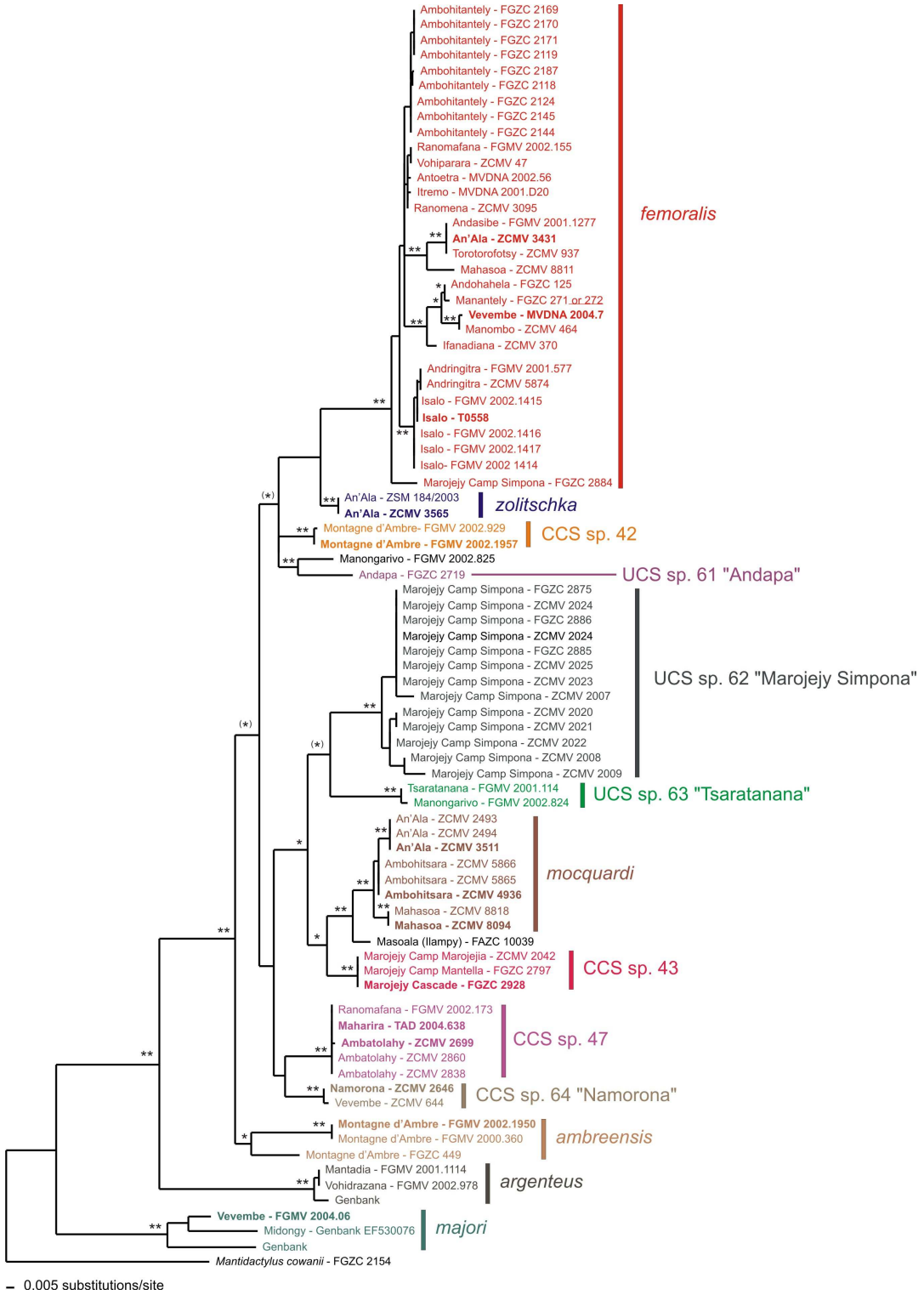

Figure 1. Bayesian inference tree calculated on the basis of up to 500 base pairs of the mitochondrial 16S rRNA gene. Asterisks denote Bayesian posterior probability values: (*), >90%; * > 95%, ** > 99%. Different species and candidate species are indicated by different colours. Sequences from tadpoles are in bold. The tree shows clusters of individuals (adults and tadpoles) assigned to species and candidate species based on their mitochondrial similarity, but was not primarily reconstructed to assess the phylogeny among *Ochthomantis* for which a more extensive multi-gene dataset would be necessary. Note that the tree does not include a few available sequences (*M. majori*, adults from Ranomafana and tadpole ZCMV 3761 from Ranomafana; *M. femoralis*, tadpole ZCMV 2640 from Ranomafana) because these contained too many missing data; species identification on the basis of these short sequences was, however, unambiguous in analyses based on an adjusted alignment of ca. 200 bp. Two adult specimens were not assigned to species or candidate species: FAZC 10039 (possibly *M. mocquardi*), FG/MV 2002.825 (possible additional UCS from Manongarivo).

understood due to the application of molecular phylogenies (*e.g.*, Glaw &Vences 2006; Glaw et al. 2006), their species-level systematics are very poorly explored, and numerous candidate species await formal description (*e.g.*, Vieites et al. 2009). Within *Mantidactylus*, the subgenus *Ochthomantis*, according to the latest revisions by Glaw & Vences (2004, 2006) currently consists of five valid species: *Mantidactylus ambreensis* Mocquard 1895; *M. femoralis* (Boulenger 1882); *M. majori* Boulenger 1896; *M. mocquardi* Angel 1929; and *M. zolitschka* Glaw & Vences 2004. Within this subgenus there is strong evidence for additional cryptic diversity, and numerous new candidate species have already been identified (Glaw & Vences 2004; Rabibisoa et al. 2008; Vieites et al. 2009). At present, three distinct species in the subgenus are relatively easy to diagnose: *M. ambreensis*, *M. majori* and *M. zolitschka*. In contrast, *M. femoralis* and *M. mocquardi* as currently understood are complexes of multiple species (Glaw & Vences, 2007).

Anuran larvae show many special and characteristic features which are distinctly different from those of the adult frog stage, encompassing ecology, morphology and habits (McDiarmid & Altig 1999). These features can also be very diverse among tadpoles, and likely are the results of adaptation to their environment. However, tadpole characters also are partly determined by the phylogenetic history of the respective species, and have successfully been used for phylogenetic reconstruction (Haas 2003).

Descriptions of anuran species, as a rule almost without exception, are based on type material in the metamorphosed, usually adult, stage. In fact, for many species – possibly from the majority of frog species worldwide – the larval stages are not reliably known. Only recently has the identification of different life-history stages of an organism by matching their DNA sequences become possible, a technique usually called DNA barcoding (Hebert et al. 2003). The application of this technique to amphibians is promising (Thomas et al. 2005; Vences et al. 2005) and allows efficient surveys of the species and larval diversity of tropical frog communities (Vences et al. 2008). In some taxonomically poorly studied frog groups the paradoxical result might be that the tadpoles are better known than the adults, both regarding their ecology and their morphology.

In other poorly known organisms such as the meiobenthic fauna, studies often end up with many taxa being only identified via their DNA sequences and not by their morphology, an approach for which Markmann & Tautz (2005) proposed the term 'reverse taxonomy'. Such a situation applies to the frogs in the subgenus *Ochthomantis*. These frogs are rather inconspicuous regarding adult morphology, and candidate species have largely been identified on the basis of DNA sequences (Vieites et al. 2009). Several of the described *Ochthomantis* species and most candidate species appear to be diagnosable as adults only by the application of detailed morphometric analyses (Rabibisoa et al. 2008). The morphology of tadpoles has not been assessed for most species of *Ochthomantis*, and it is thus far unknown whether tadpole characters might perform better in species discrimination than adult morphology. So far, only tadpoles assigned to

Figure 2. Diversity of adults in the *Mantidactylus* subgenera *Maitsomantis* (M. *argenteus*) and *Ochthomantis*. Morphological identification of several species is unambiguous: *Mantidactylus argenteus* (FG/MV 2002.537 from Ranomafana), M. *majori* (specimen from Ranomafana, not collected), M. *ambreensis* (specimen from Montagne d'Ambre), M. *zolitschka* (paratype ZFMK 60116 from An'Ala). Others were identified by DNA barcoding, i.e., on the basis of the molecular tree in **Figure 1**: M. *femoralis* (FG/MV 2002.56 from Antoetra); M. *mocquardi* (ZCMV 5865 from Ambohitsara), M. sp. 63 (specimen from Tsaratanana), M. sp. 62 (ZSM 309/2005-FGZC 2885 from Marojejy, Camp Simpona), M. sp. 61 (ZSM 221/2005-FGZC 2719 from Andapa), M. sp. 42 (specimen from Montagne d'Ambre, assignment to this confirmed candidate species is tentative and not based on molecular data), M. sp. 43 (ZSM 253/2005-FGZC 2797 from Marojejy Camp Mantella), M. sp. 47 (specimen from Ambatolahy).

M. femoralis have been briefly described by Blommers-Schlösser (1979) and a larva of an unidentified species from the Chaines Anosyennes (1060 m a.s.l.), probably referable to the subgenus *Ochthomantis*, was briefly characterized by Blommers-Schlösser & Blanc (1991).

In contrast to the uniform and conspicious adult morphology of *Ochthomantis*, their tadpoles have unique specialized mouthparts which make them easy to distinguish from tadpoles of other mantellid genera and subgenera. Their oral disk is characterized by *(1)* a strong reduction of the number of labial tooth rows and the density of labial teeth, and *(2)* a reduction of the keratinisation of the jaw sheaths. Such divergent oral disk structures probably are specializations either on particular food items and/or feeding behavior. In general, such specialized larval adaptations may be one key to understand the high diversity of tropical amphibian communities (Strauß et al. 2010).

In this study, we provide descriptions of the external morphology of the tadpoles of ten species of *Mantidactylus* (*Ochthomantis* and *Maitsomantis*), eight of them for the first time. We here do not include details of buccal anatomy or microstructures such as labial teeth on which we will focus in a future comprehensive survey of tadpole buccal cavities in the Mantellidae. We assign species and candidate species to three separate morphological clusters on the basis of external tadpole morphology, and discuss the evolution of specialization of oral structures in *Ochthomantis* as well as the advantages of DNA barcoding for identifying tadpoles.

Material and methods

1. Morphological study of tadpoles

Tadpoles were collected using different types of nets having mesh sizes from 2 to 5 mm, depending on the size of the streams, the strength of the current and the type of substrate. They were euthanized by immersion in chlorobutanol solution, and immediately sorted into homogeneous series based on morphological characters. From each series one specimen was selected and a tissue sample from its tail musculature or fin taken and preserved in 99% ethanol. This specimen is here called 'DNA voucher'. All detailed morphological tadpole characterizations and drawings are based on this DNA voucher, whereas observation for the variation refer to further DNA voucher specimens from the same locality or from different localities, and sometimes to the non-sequenced specimens of the same series. After tissue collection, all specimens were preserved in 5% formalin or 70% ethanol. Specimens were deposited in the Zoologische Staatssammlung München, Germany (ZSM). When referring to voucher specimens the original field numbers

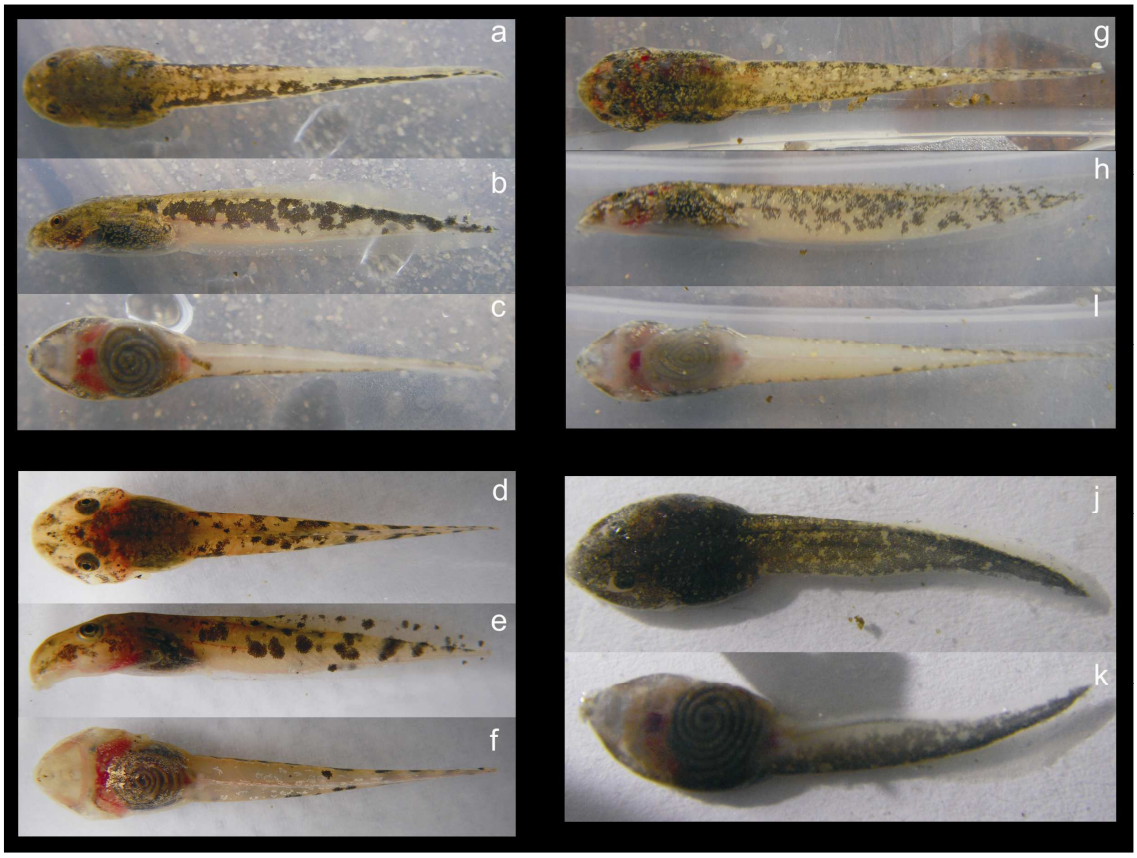

Figure 3. Colouration in life of tadpoles of four species in the *Mantidactylus* subgenus *Ochthomantis*, all collected in Ranomafana National Park and surroundings. M. *femoralis* (ZCMV 3821 – ZSM 188/2008): **a** – dorsal view; **b** – lateral view; **c** – ventral view. M. *majori* (T 09/746, to be catalogued in ZSM): **d** – dorsal view; **e** – lateral view; **f** – ventral view. M. sp. 47 (ZCMV 3791 – ZSM 506/2008): **g** – dorsal view; **h** – lateral view; **i** – ventral view. M. sp. 64 (ZCMV 9291, to be catalogued in ZSM): **j** – dorsal view; **k** – ventral view.

FAZC, FGZC, T, TAD, ZCMV) are usually provided together with the final ZSM catalogue numbers. Tadpoles were identified using a DNA barcoding approach (see below). Tadpoles studied in this paper are listed in Appendix 2-Table 3 including data concerning the site and its coordinates, the date of the capture and the collectors.

For detailed morphological examination, especially to determine developmental stages and assess characters of the oral disk, preserved tadpoles were stained slightly with methylene blue. Tadpoles were examined under water and few drops of methylene blue were applied to the oral disk, hind limb, spiracle, narial opening, and vent tube for having a better view of their structure. Developmental stages are determined following Gosner (1960). Description, measurements and drawings were done on digital pictures of the preserved tadpoles taken with a Stereomicroscope Zeiss Discovery V12 connected to a computer, following the landmarks, terminology and definitions of McDiarmid & Altig (1999). New landmarks are also introduced herein (Figure 9). Developmental stages are described following Gosner (1960). The formula of labial tooth rows (LTRF) is given according to Altig & McDiarmid (1999). Labial teeth are also referred to as keratodonts following Dubois (1995). When describing interruptions of keratodont rows we considered these as scattered when they have more than a single medial interruption. Drawings of the preserved tadpoles are shown in the Appendix. When categorizing morphometric ratios, we consider them as "almost equal" if ratios of the measured values are 95-96% or 104-105%, as "equal" if they are in the range 97-103%, as "almost in the middle" if they are in the range 45-46% or 54-55% and as "in the middle" if they are in the range 47-53%.

The following abbreviations are: A_1 (first upper keratodont row), A_2 (second upper keratodont row), A_{2gap} (medial gap in A_2), A_3 (third upper keratodont row), $A_{1\text{-}3\ den}$ (density of the keratodonts in $A_{1\text{-}3}$), $A_{1\text{-}3\ len}$ (length of $A_{1\text{-}3}$), $A_{1\text{-}3\ num}$ (number of keratodonts in $A_{1\text{-}3}$), BH (maximal body height), BL (body length), BW (maximal body width), DF (dorsal fin height at midtail), DG (size of the dorsal gap of marginal papillae), DMTH (distance of maximal tail height from the tail-body junction), ED (eye diameter), EH (eye height – measured from the lower curve of the belly), HAB (height of the point where the axis of the tail myotomes contacts the body – measured from the lower curve of the belly), IND (inter-narial distance), IOD (inter-orbital distance), JW (maximal jaw sheath width), MC (medial convexity of the upper sheath), MCL (length of the medial convexity of the upper sheath), MP (marginal papillae), MTH (maximal tail height), ND (naris diameter), NH (naris height – measured from the lower curve of the belly), NP (naris-pupil distance), OD (oral disk), ODW (maximum oral disk width), P_1 (first lower keratodont row), P_2 (second lower keratodont row), P_3 (third lower keratodont row), $P_{1\text{-}3\ den}$ (density of the keratodonts in $P_{1\text{-}3}$), $P_{1\text{-}3\ len}$ (length of $P_{1\text{-}3}$), $P_{1\text{-}3\ num}$ (number of keratodonts in $P_{1\text{-}3}$), R/L (right/left), RN (rostro-narial distance), SBH (distance between

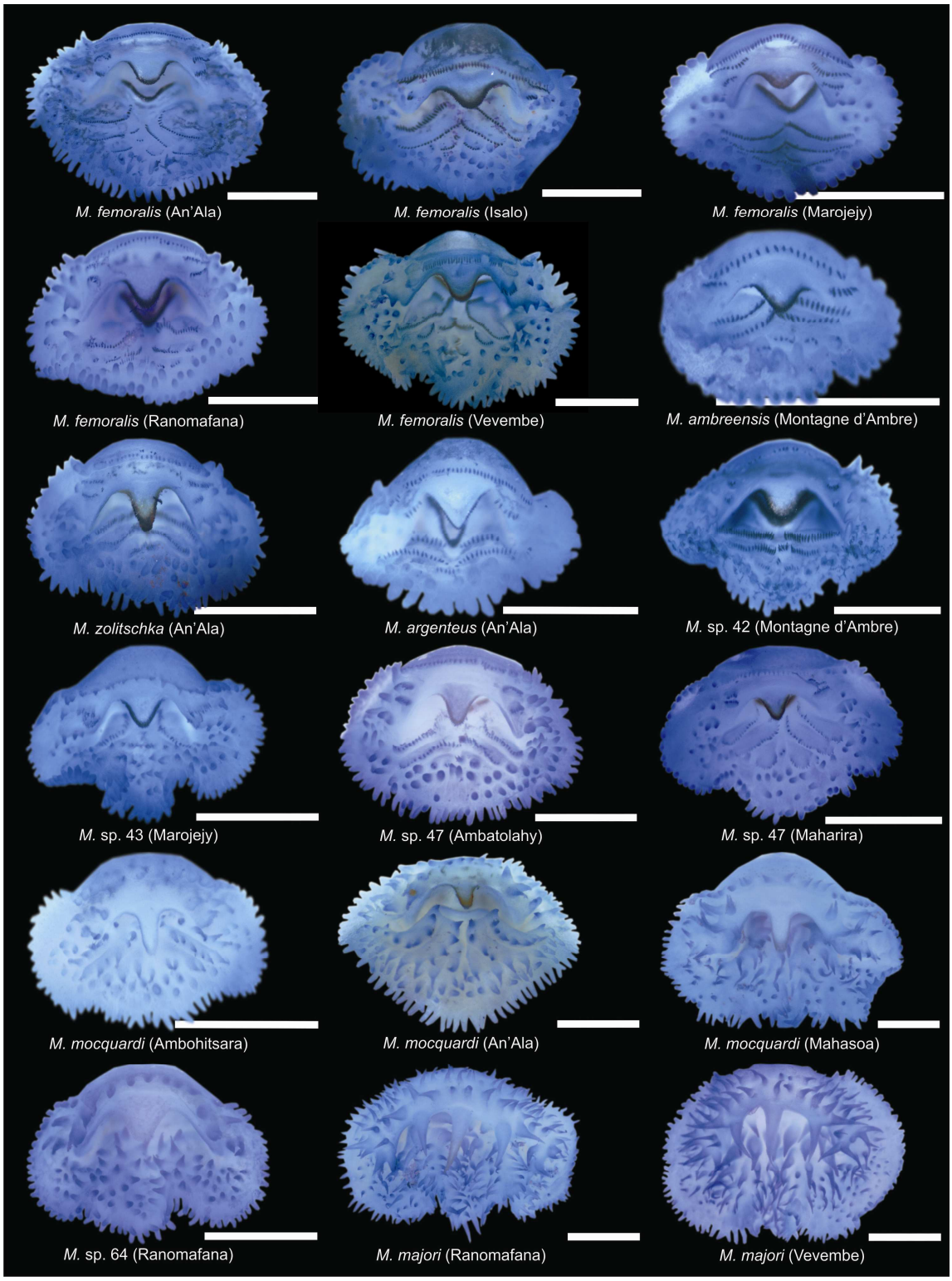

Figure 4. Photographs of the oral disk of the preserved voucher specimens of *Mantidactylus* subgenus *Ochthomantis* tadpoles described in this paper (stained with methylene blue). The scale bars represent 1 mm.

snout and the point of maximal body height), SBW (distance between snout and the point of maximal body width), SE (snout-eye distance), SH (spiracle height – measured from the lower curve of the belly), SL (spiracle length), SMP (submarginal papillae), SS (snout-spiracle distance), SV (spiracle-vent distance), TAL (tail length), TH (tail height at the beginning of the tail), THM (tail height at mid-tail), Thorn-pap (thorn-shaped papillae), TL (total length), TMH (tail muscle height at the beginning of the tail), TMHM (tail muscle height at mid-tail), TMW (tail muscle width at the beginning of the tail), LR (number of the lower rows of keratodonts), UR (number of the upper rows of keratodonts), VF (ventral fin height at midtail), VG (size of the ventral gap of marginal papillae), VL (vent tube length).

2. Molecular analyses

DNA barcoding was based on a fragment of the mitochondrial 16S rRNA gene, which is known to be sufficiently variable among species of Malagasy frogs (Vences et al. 2005). We amplified a fragment of ca. 550 bp using primers 16Sar-L and 16Sbr-H from Palumbi *et al.* (1991), or a shorter fragment of ca. 400 bp using the newly developed specific mantellid primers 16S-Frog-L1 (CAT AAT CAC TTG TTC TTT AAA) and 16S-Frog-H1 (GAT CCA ACA TCG AGG TCG). PCR was carried out with standard protocols (Vences et al. 2003) and sequences resolved on automated sequencers. Sequences were preliminarily identified using BLAST searches against a near-complete database of sequences of adult Malagasy frog species. Results were subsequently verified by manually aligning and comparing sequences to the closest hits in the data base. Identification was considered to be unequivocal when the tadpole sequence was 99–100% identical to an adult specimen from the same geographical region, and clearly less similar to all sequences from other species. When no identity with adult specimens was found and divergence was >3% we considered the corresponding tadpoles to belong to additional candidate species, a situation that arose in a single case. DNA sequences were deposited in Genbank (accession numbers of newly determined DNA sequences HQ610836-HQ610924).

To visualize the molecular relationships among adult and larval *Ochthomantis*, sequences were aligned by eye. We performed a Bayesian phylogenetic analysis using the program Mrbayes 3.1 (Ronquist & Huelsenbeck 2003). We used MrModeltest version 2.2 (Nylander 2004) to choose the appropriate model of sequence evolution. Analyses consisted of four Markov chains that ran for 5 millions of generations, sampled every 1000 generations, with a random starting tree and default priors.

The burn-in was empirically estimated by plotting –ln L against the generation number, and the trees corresponding to the first 4 million generations discarded. Based on more extensive studies of the phylogeny of mantellids (Glaw & Vences 2006; Glaw et al. 2006) we included in

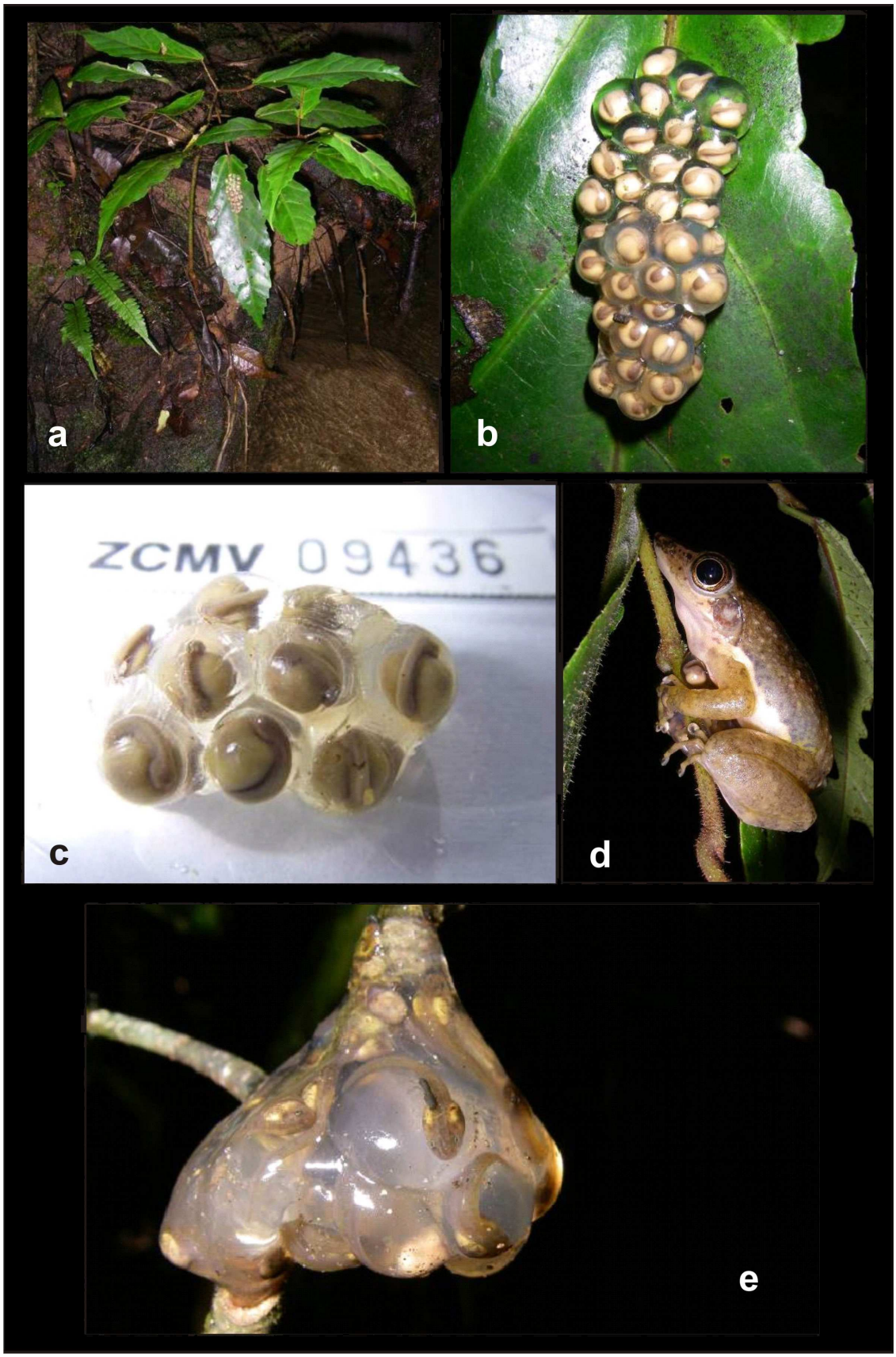

Figure 5. Clutches and egg guarding behaviour of *Mantidactylus majori*: **a** – and **b** – show a clutch (ZCMV 9436) attached to a leaf, 40 cm above water body (Ranomafana, Ambatovory Barrage); **c** – shows a part of the same clutch; **d** – shows an adult *M. majori* guarding a clutch attached to vegetation about 80 cm above water body (Ranomafana, Ambatolahy); **e** – shows a clutch of *M. majori* (ZCMV 9537, no ZSM) with well developed tadpoles attached to a branch about 1 m above water body (Ranomafana, Sahamalaotra bridge).

our analysis *Mantidactylus* (*Maitsomantis*) *argenteus* which is closely related to *Ochthomantis*, and used *Mantidactylus* (*Hylobatrachus*) *cowanii* as the outgroup because *Hylobatrachus* has been recovered previously as member of the sister clade of *Ochthomantis*+*Maitsomantis* (Glaw et al. 2006).

3. Habitat preference analysis

In the framework of a study on stream tadpole communities in the Ranomafana National Park (RNP) in the Southern Central East of Madagascar, breeding site choice and tadpole microhabitat preferences were evaluated at 33 stream sections.

To evaluate the correlation of habitat (stream) characteristics with breeding site choice of *Ochthomantis* species (*i.e.*, tadpole occurrence), the following habitat variables of the streams and their surrounding forest area were recorded: slope, width, depth, overhanging vegetation, and canopy cover of the stream; the density of shrubs, small trees, large trees, depth of forest floor leaf litter, slope of the forest floor, and canopy cover of the forest (exact definitions of these variables are in Strauß et al. 2010).

For each stream, 30 m long stream sections were as exhaustively as possible sampled for tadpoles, separately for all available microhabitats within the section. These microhabitats were predefined based on the structure of the ground substrate (categories rock, gravel, leaves, sand) and by stream velocity, with the categories 'fast' (obviously running) and 'slow' (almost stagnant) resulting in eight different possible types of microhabitat. To test for microhabitat preferences, the frequency of the microhabitats available was recorded for each stream. For details of sampling methods see Strauß et al. (2010).

Tadpole sampling was conducted in the wet season (January and February) 2008 and repeated in a subset of the streams during the dry season (July) 2008. Statistical analyses were exclusively based on data from the rainy season as both the presence and abundance of *Ochthomantis* tadpoles during the dry season were very limited. Analysis were performed in R 2.9.2 (R Development Core Team 2009) including library car (Fox 2008).

To identify the habitat variables of the stream and the surrounding forest that correlate with the presence of *Ochthomantis* tadpoles (all species pooled), first a principal component analysis (PCA) was performed. PCA was performed on the correlation matrix in order to standardise for the influence of unequal variance.

To evaluate data outliers and linear interdependence of variables, box-plots and pair-plots (Zuur et al. 2007) were used. As PCA requires multinormality of data, box-cox-power-transformations (Box & Cox 1964) were applied when necessary. The significance of the PC

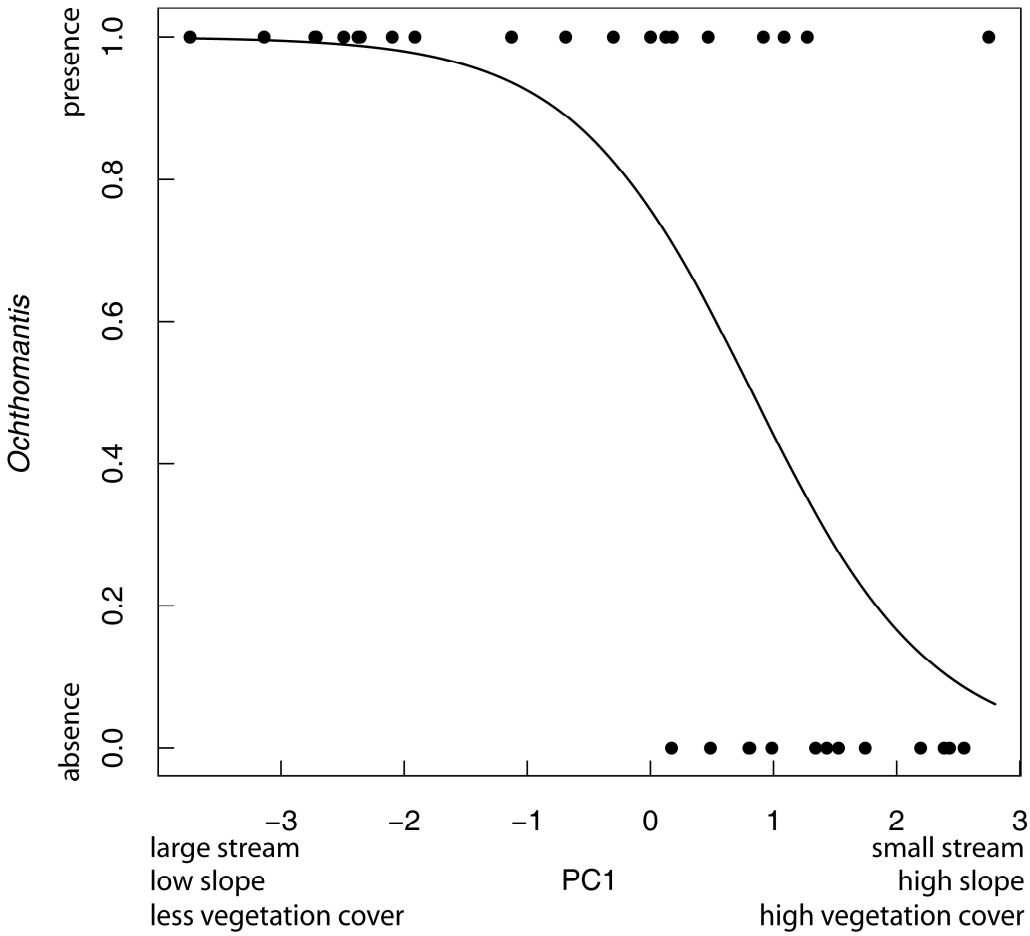

Figure 6. Presence and absence of *Mantidactylus* subgenus *Ochthomantis* tadpoles in streams of RNP along the PC1 gradient. PC1 explains 34% of the variation in the original data. Each point represents a stream, the regression line of the logistic regression is plotted.

loadings was assessed based on the bootstrapped-eigenvector method as suggested by Peres-Neto et al. (2003). The number of meaningful PCs was estimated by a scree plot (Zuur et al. 2007). A multiple logistic regression (generalized linear model, GLM, with binomial errors) with the first three PCs as independent variables and the presence/absence of *Ochthomantis* tadpoles as binary dependent variable was performed to extract the key habitat variables important for breeding site choice of *Ochthomantis* frogs. Independent terms and interaction terms were deleted sequentially from the full model based on the Akaike Information Criterion (Burnham & Anderson 1998) until the minimum adequate model was reached.

In order to quantify microhabitat preference of *Ochthomantis* tadpoles within streams, Ivlev's electivity index E (Ivlev, 1961) was calculated for each *Ochthomantis* species occurring in RNP. E is defined as E=(r-p)/(r+p) with r being the proportions of the microhabitats used (using tadpole abundance) and p the proportion of microhabitats available. To test whether the E values differ between the single species, a factorial ANOVA was run with E as dependent variable and the factors 'species' and 'microhabitat' as independent variables. This provides information whether E is different for the different microhabitats and whether observed differences vary between species. Only the three abundant species were included in this analysis.

Results

1. Larval and adult diversity in *Ochthomantis*

The molecular tree of 81 adults and larvae of the *Mantidactylus* subgenera *Ochthomantis* and *Maitsomantis* (Figure 1) supports previous conclusions (Glaw & Vences 2004; Vieites et al. 2009) of a high undescribed species diversity of *Ochthomantis*. Adult specimens of all described species in the genus (*M. ambreensis*, *M. femoralis*, *M. majori*, *M. mocquardi*, *M. zolitschka*) were recovered as monophyletic and genetically distinct groups, together with their respectively assigned tadpoles. In addition, several clusters were identified that we here define as candidate species according to the terminology and criteria of Vieites et al. (2009). Although the tree provides significant Bayesian posterior probabilities for various relationships among species in the subgenus *Ochthomantis*, we emphasize that its purpose is not to provide a phylogenetic hypothesis but merely to visualize molecular differentiation among clusters of individuals that correspond to species and candidate species.

Because we were able to assign adult specimens (Figure 2) and larvae (Figure 3) to most of the molecular clusters, we understand which of these are supported as evolutionary independent

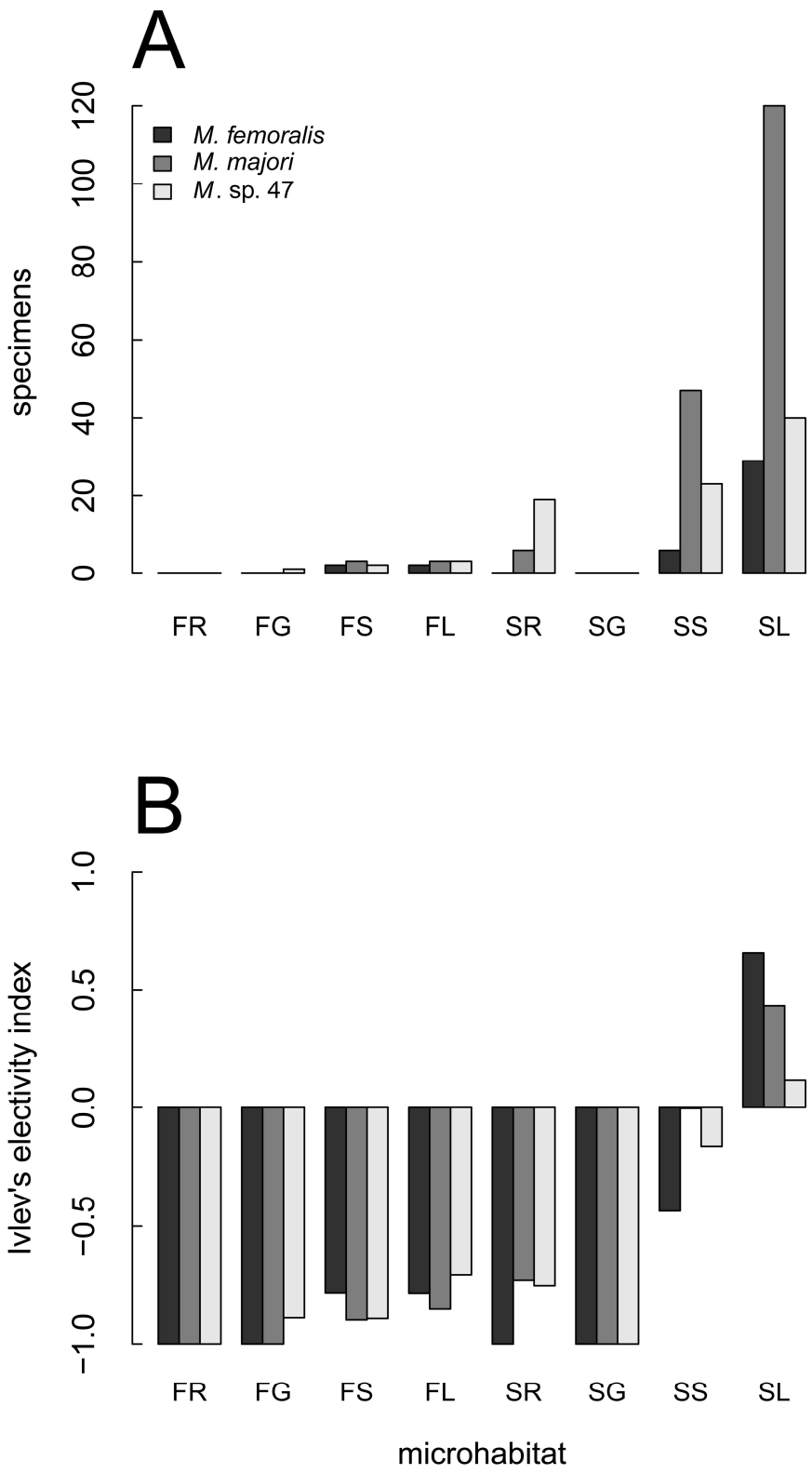

Figure 7. Habitat use and habitat preferences of the three abundant species of *Mantidactylus* subgenus *Ochthomantis* sampled in January and February 2008 in Ranomafana National Park. Plotted is (A) the distribution of specimens and (B) Ivlev's electivity index (Ivlev, 1961) across eight microhabitats (FR= fast rocks, FG= fast gravel, FS= fast sand, FL= fast leaves, SR= slow rocks, SG= slow gravel, SS= slow sand, SL= slow leaves). Negative values show avoidance, positive values preferences for the respective microhabitat. $N_{M.\ femoralis}$=7, $N_{M.\ majori}$=11, and $M_{M.\ sp.\ 47}$=16 (N is the number of streams where the species was found). The general low values in (B) are caused by a high number of non-occurrence events in the specific microhabitats in some streams.

units by the congruence of independent data sets, mainly larval morphology and mitochondrial DNA sequences. Consequently, we defined as confirmed candidate species (CCS) those where congruent molecular and morphological results were available. Others were only identified as molecular clusters (with pairwise 16S divergences of >3% to other clusters; Vieites *et al.*, 2009) without additional evidence from morphology of tadpoles, or morphology or bioacoustics of adults, and are therefore defined as unconfirmed candidate species (UCS). Both CCS and UCS were named following Vieites et al. (2009) who numbered all candidate species in *Mantidactylus* from 1-60. The four additional candidate species identified herein are consecutively numbered 61-64. While the present study was under review, a publication by Padial et al. (2010) proposed a new scheme for naming candidate species. We endorse this new proposal and will apply it in further studies, but have here refrained to apply it yet to candidate species in *Ochthomantis* because we felt that consistency with the candidate species names of Vieites et al. (2009) is preferable at this point of time.

The following accounts briefly characterize the various species and candidate species by their larval and adult morphology, as far as currently possible. Detailed descriptions of the tadpoles are provided in the appendix, measurements and morphometric ratios of DNA voucher specimens in Appendix 3-Table Tables 7, 8, and 9, a comparison of the main morphological features of the different species in Table 5, and a summary of collection localities and specimens examined in Appendix 2-Table 3. Interestingly, in *Ochthomantis*, larval characters especially of the oral disk proved to be highly derived in all species and provided various clear morphological differences among species, whereas morphological differentiation of adults is more subtle (see also Glaw & Vences 2004; Rabibisoa et al. 2008). In the following, species are therefore roughly listed by their degree of larval specialization. We first provide some detailed morphological data for one of the least specialized species, *Mantidactylus femoralis*,and then highlight distinctive features and specializations of the other species.

Mantidactylus femoralis

Following Glaw & Vences (2004) we define *M. femoralis* as the most widespread and most common species in the subgenus *Ochthomantis*. Adults of this species are characterized by medium size, a more or less tubercular back, and a distinct and often rather large yellow inguinal patch (Figure 2). According to the molecular data herein, this species is known from the South East (Andohahela, Manantantely, Vevembe, Manombo) to the North East (Marojejy), including many localities in the intervening areas (in a south-north direction: Andringitra; Isalo; Antoetra; Itremo; Ifanadiana; Ranomafana including Vohiparara, Ranomena and other sites; An'Ala; Andasibe; Torotorofotsy; Ambohitantely; Mahasoa).

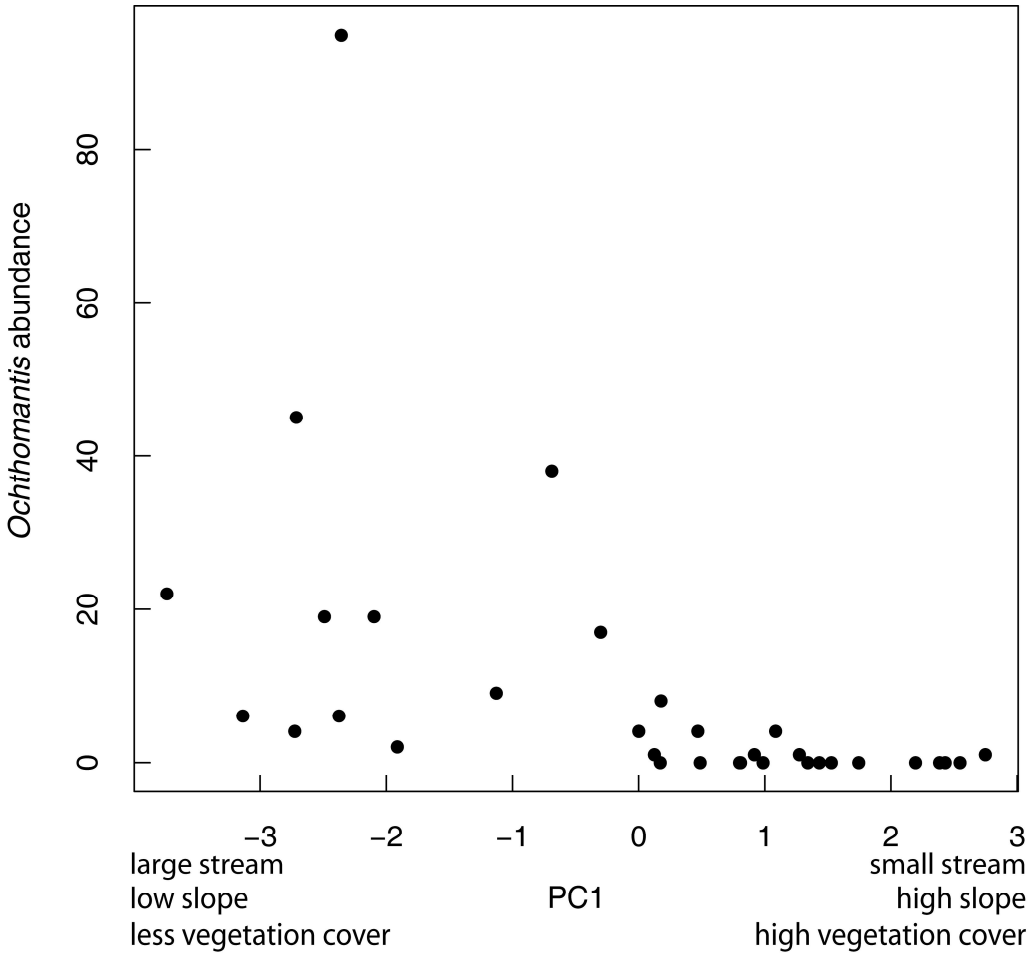

Figure 8. Abundance of *Mantidactylus* subgenus *Ochthomantis* tadpoles in streams of RNP along the PC1 gradient. PC1 explains 34% of the variation in the original data and represents a gradient from bigger, open streams towards smaller streams with higher slope at sites with high vegetation cover. Each point represents a stream.

The tadpole of *M. femoralis* (based on ZSM 1736/2007-ZCMV 3431, Gosner stage 28 from An'Ala (see appendix and Fig. 10 for preserved tadpole) and on ZSM 188/2008-ZCMV 3821 from Ranomafana (Figure 3 for tadpole in life) has an elliptical body, a narrowly rounded snout in dorsal view and a constriction behind the point where the maximal body width is attained (between the proximal 2/5 and 3/5 of the body). In lateral view the body is depressed; the maximal body height is attained between the proximal 3/5 and 4/5 of the body; and the snout is narrowly rounded. Eyes are small, not visible in ventral view, positioned high dorsally and directed laterally, and situated between the proximal 3/10 and 4/10 of the body. The distance between the eyes is moderately wide. Nares are small, rounded, marked with a marginal rim, positioned high dorsally and oriented anterolaterally, situated nearer to snout than to eye and below eye level. The distance between nares is moderately wide. A red patch is present on the back of the nares. The spiracle is sinistral, moderately large, directed posteriorly, visible from dorsal and ventral views, and perceptible from lateral view. Its inner wall is free from the body and formed such that the aperture opens posteriorly. The opening is rounded, situated between the proximal 3/5 and 4/5 of the body, located high and at the height of the point where the axis of the tail myotomes contacts the body. The vent tube is dextral, moderately long, attached to the ventral fin and its inner wall is present. The tail is short; the caudal musculature is moderately developed; the tail muscle reaches the tail tip. Fins are very low; the dorsal fin originates on the tail muscle on the proximal 1/5 of the tail and the ventral fin originates at the ventral terminus of the body. The maximal tail height is located at a position after the proximal 2/5 of the tail. The lateral tail vein and the myosepta are slightly visible on the proximal 3/4 of the tail musculature, the point where the axis of the tail myotomes contacts the body is high and the axis of the tail myotomes is parallel with the axis of the trunk. The tip of the tail is narrowly rounded.

The oral disk (Figure 4) is moderately large, reduced, not emarginated, positioned ventrally, and directed anteroventrally. It is visible in dorsal view and the upper labium is a continuation of the snout. There is a single row of marginal papillae interrupted by a wide gap on the upper labium and the gap on the lower labium is absent. There are 59 marginal papillae and 69 submarginal papillae which are complete on the lower labium and laterally on the upper labium. Very short but moderately wide papillae with rounded tips exist and the longest marginal and submarginal papillae measure 0.08 mm. Papillae are visible in dorsal view. LTRF is 3(2-3)/3(1-2). A_1 is moderately long and the density of its keratodonts is 39/mm. The gap in the first upper interrupted row is wide. Lower keratodont rows form a chevron, P_1 and P_2 are interrupted and P_2 and P_3 are scattered. Keratodonts are very short and distinguishable. Distal keratodonts have the same lengths as those in the center. There is considerable space between marginal papillae and keratodont rows. Jaw sheaths are moderately wide and poorly keratinized. The upper sheath has a short widely rounded medial convexity. The edge of the medial convexity is black

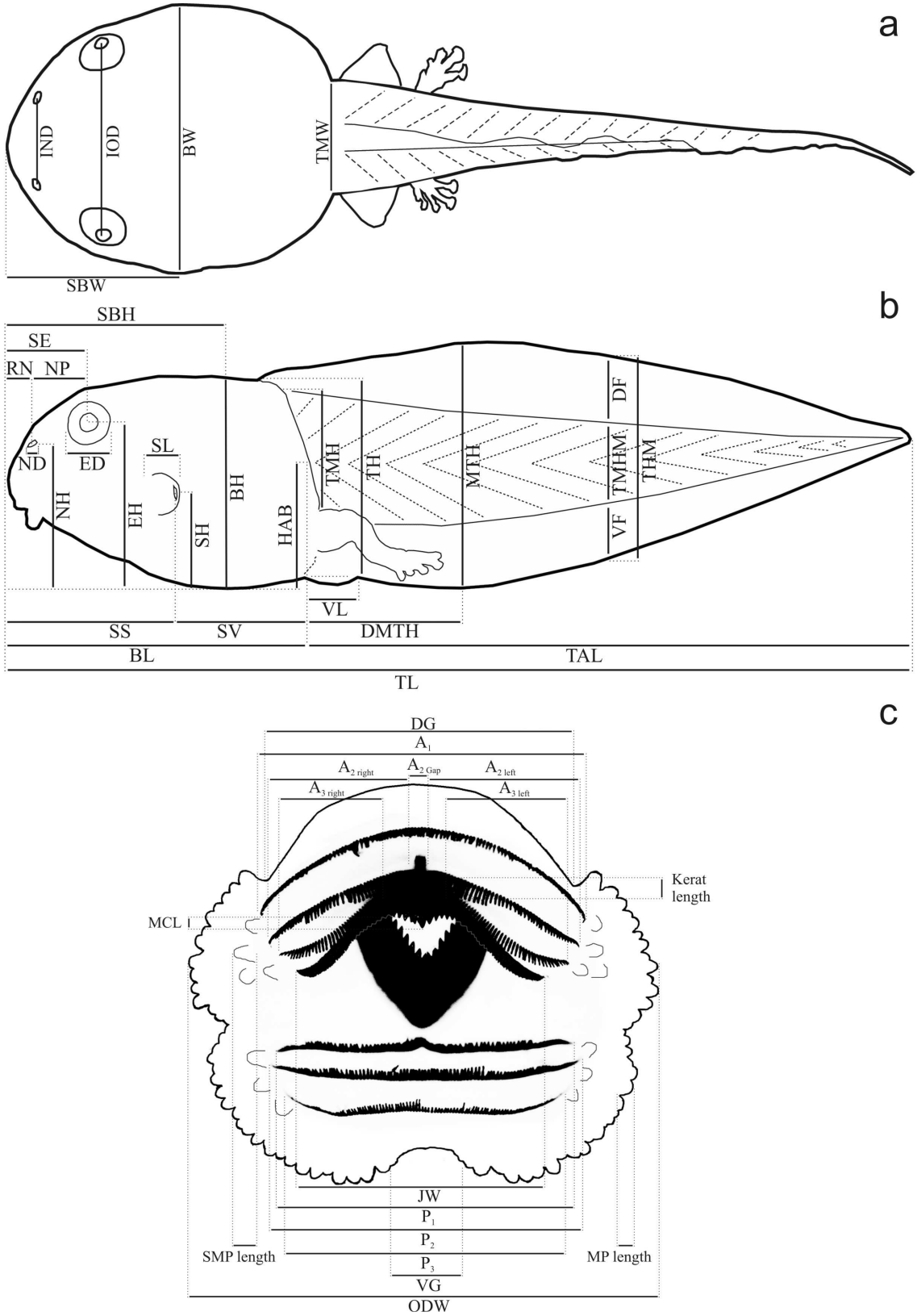

Figure 9. Drawings representing the landmarks of the measurement: **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

colored and the remainder is whitish. Serrations are finely pointed. The lower sheath is V-shaped, partially keratinized and totally hidden by the upper one.

In life, the tadpole is generally uniformly dark (Figure 3). Dorsal sides of the head and trunk are covered by dark patches and gold blotches. Ventrally, oral disk and gular regions are transparent, the branchial region is reddish, and the abdominal surface is transparent. The tail musculature is yellow-reddish and covered by brown reticulations. Fins are transparent and the dorsal fin has brown reticulations. In preservative, the tadpole is uniformly dark brown. Brown pigment is positioned in deep integumental layers and covers the dorsum and flank of the body. Some dark brown patches are scattered on the dorsal skin. Ventrally, the oral disk, gular and branchial regions are patched; the abdominal surface is pale. The intestinal coils are perceptible and regular spiral shaped. The lower part of the flanks has the same coloration as ventrally and the intestinal coils are perceptible laterally. The tail musculature is overlain by dark brown reticulations. Fins are pale; the dorsal fin is covered with sparse brown reticulations.

Six DNA voucher specimens from the same locality, eight DNA voucher specimens from Ranomafana National Park, one DNA voucher specimen from Vevembe forest and one DNA voucher specimen from Isalo National Park attributed to *M. femoralis* show the same oral disk morphology (Figure 4), but one tadpole from Ranomafana National Park differs by its LTRF of 2(2)/3(1-2). A single tadpole from Marojejy National Park assigned to *M. femoralis* (by molecular data) differs by some variables like its lower numbers of only 43 marginal and 30 submarginal papillae.

Mantidactylus ambreensis

A species easily recognizable by its adult coloration (Figure 2), with a rather uniform dark brown dorsum with a continuous white (rarely yellowish) lateral line. This species is known from the North (Montagne d'Ambre) and Sambirano regions (Benavony, western slope of the Tsaratanana massif; Glaw and & Vences 2007). We have also recently collected specimens from the western slopes of the Makira plateau near Mandritsara (own, unpublished data). The tadpole of this species (based on ZSM 762/2004-FG/MV 2002.1950, Gosner stage 25 from the type locality Montagne d'Ambre National Park; see Figures 4 and 11) is differentiated from *M. femoralis* by its beige-brownish coloration in preservative (no data on life coloration is available). The dorsal sides of the head and trunk and the higher part of the flank are beige with light brown reticulations between nares and eyes, on the frontal and along the vertebral area. The tail musculature is beige with brown blotches which fuse in some areas to form a network. Differences are also found regarding the body form in dorsal view, the size of the eyes and nares, the distance between the eyes and between the nares, the direction of the spiracle, the location of

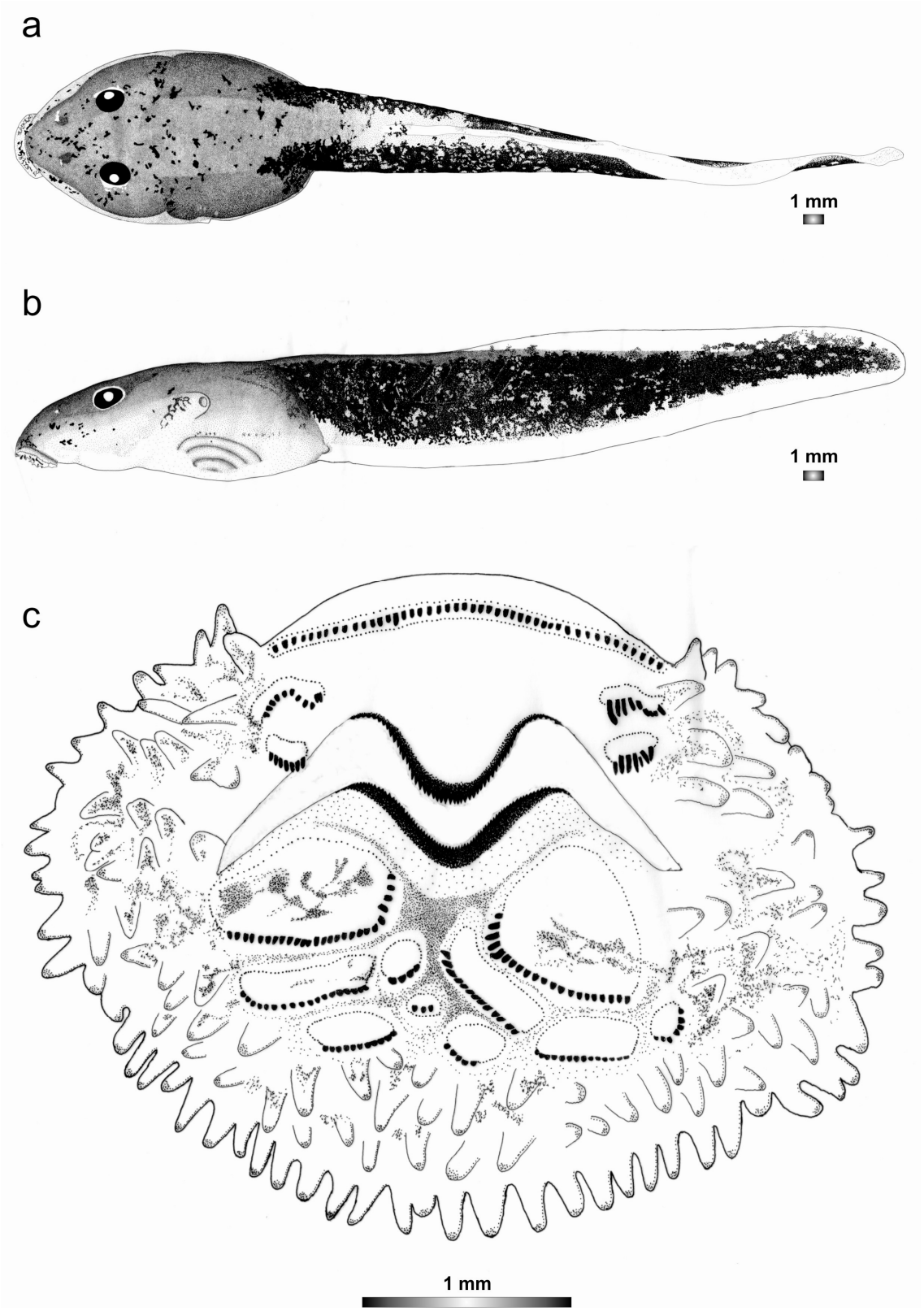

Figure 10. Drawings of the preserved DNA voucher tadpole of *Mantidactylus femoralis* (ZCMV 3431-ZSM 1736/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

the spiracle opening, the length of the vent tube and the tail, the origin of the dorsal fin, the size of the caudal musculature, the visibility of the myosepta and the oral disk, the number of papillae, the state of P_2, the LTRF which is 2(2)/3(1-2), the density of keratodonts in A_1, the size of the gap in A_2, and the shape of the medial convexity. The examination of four additional specimens belonging to the same series (but not identified by DNA barcoding) revealed similar morphological characteristics, mainly in the oral structure, but the LTRF showed some variation: 2(2)/3(1-2) and 3(2-3)/3(1-2).

Mantidactylus zolitschka

So far this species, characterized mainly by its rather small adult size and low sexual size dimorphism (Glaw & Vences 2004) is only known from its type locality, An'Ala. Its tadpole (based on ZSM 1843/2007-ZCMV 3565, Gosner stage 27 from An'Ala; see Figures 4 and 12) is characterized by the faintness of the pigmentation of the keratodonts and the narrow elongated shape of the upper jaw sheath. The external morphology of the tadpoles differs from that of the tadpoles of *M. ambreensis* by body size, external pattern and coloration, LTRF, number of papillae and the configuration of the medial convexity. The tadpoles of *M. zolitschka* are similar to those of *M. femoralis* by the presence of a small constriction at midbody, but they can be differentiated by their coloration in preservative (no data on life coloration is available). *Mantidactylus zolitschka* tadpoles are generally beige-brownish with a light brown network of pigments positioned in deep integumental layers. These pigments cover the major surface of the dorsal sides of the head and trunk and the flank. Dark brown spots form patches which are scattered on the dorsal skin. Dark brown spots coalesce to form networks which are scattered irregularly on the tail musculature. Further differences to *M. femoralis* are the shape of the snout, the size and the direction of the eyes, the presence of reddish patches on the back of the nares, the distance between the nares and their direction, the location of the spiracle opening, the size of the caudal musculature, the origin of the dorsal fin, the visibility of the myosepta and the lateral tail vein, the shape of the tail tip, the direction of the oral disk, the size of the dorsal gap of the marginal papillae, the number of marginal and submarginal papillae, the shape and the size of papillae, the density of keratodonts on A_1, the state of P_2, and the size and shape of the upper jaw sheath. Four DNA voucher specimens from the same locality attributed to *M. zolitschka* show the same oral disk configuration and pigmentation, one tadpole having a different LTRF, 2(2)/3(1-2).

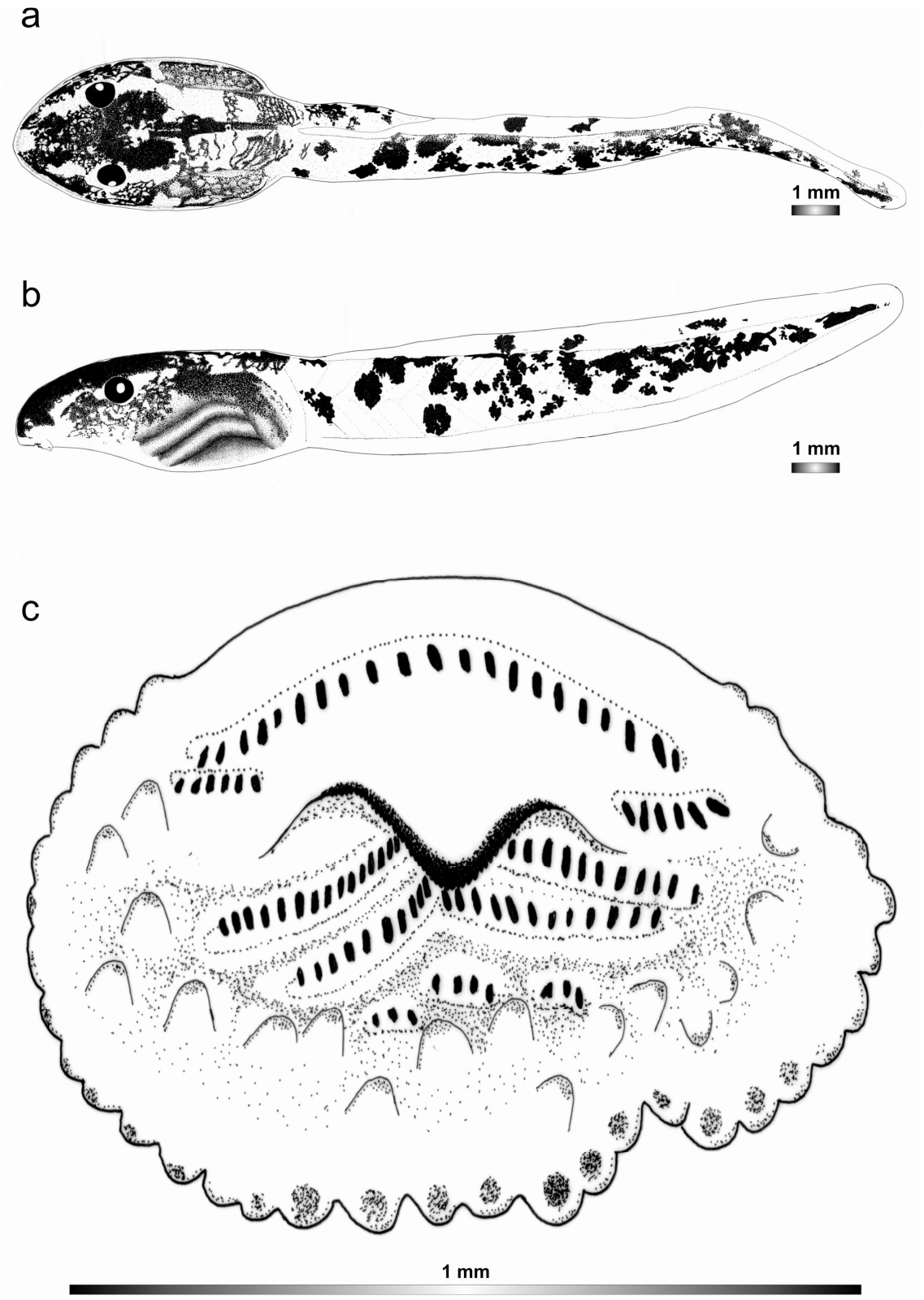

Figure 11. Drawings of the preserved DNA voucher tadpole of *Mantidactylus ambreensis* (FG/MV 2002.1950-ZSM 762/2004): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

Mantidactylus argenteus

This species, classified in a separate subgenus *Maitsomantis*, is characterized by a very distinct adult morphology with a small body size, greenish dorsal color, and very large and semitransparent tympanum in males. However, its larva (already described previously by Vejarano *et al.*, 2006) is in general similar to that of species of *Ochthomantis*: The tadpole (based on ZSM 1573/2007-ZCMV 3575, Gosner stage 27 from An'Ala; see Figures 4 and 13) is charcterized by *(1)* its unique coloration: presence of transversal clear bands between nares and eyes, between eyes and spiracle and before the body-tail junction, and a longitudinal clear band on the tail dorsum, *(2)* the protuberated snout, and *(3)* its small eyes and short spiracle. This tadpole is similar to that of *femoralis*-like tadpoles (and differs from the *mocquardi*-like, *M. mocquardi* and M. sp. 64, and the *majori* tadpoles) by the presence of labial teeth. The general configuration of the oral disk of *M. argenteus* tadpoles is similar to that of *femoralis*-like tadpoles (*M. femoralis*, *M. ambreensis*, *M. zolitschka*, M. sp. 42, M. sp. 43 and *M.* sp. 47), except a few characteristics, like the the low number of papillae. The LTRF 2(2)/3(1-2) is similar to that of *M. ambreensis* and *M.* sp. 43, but the upper sheath configuration (narrowly pointed) is similar to that of *M. zolitschka*.

Mantidactylus sp. 42

This candidate species has so far been recorded only from Montagne d'Ambre. Diagnostic features of the adult are not well understood since it cannot be excluded that more than one species of the subgenus *Ochthomantis* occur in Montagne d'Ambre (in addition to *M. ambreensis*). The single tadpole assigned to M. sp. 42 (ZSM 774/2004-FG/MV 2002.1957, Gosner stage 28 from Montagne d'Ambre National Park; see Figures 4 and 14) resemble *M. femoralis* tadpoles regarding the LTRF 3(2-3)/3(1-2) and its general coloration except the low density of the reticulations on the tail musculature and the clear surface on the dorsum in preservative (no data on life coloration is available). Some parameters like the shape of the snout in lateral view, the location of the spiracle opening, the tail length, the origin of the dorsal fin, the direction of the oral disk, the size of the dorsal gap of the papillae, the low number of papillae, the shape and the size of the papillae, the size of A_1 and the density of its papillae, and the size of the gap on the A_2 also appear to differentiate the tadpoles of these two species. *Mantidactylus* sp. 42 tadpoles have high similarities to those of *M. ambreensis* in their external pattern and coloration but they can be differentiated generally by larger body size, the LTRF with three instead of two upper keratodont rows, and the number of papillae. *Mantidactylus* sp. 42 tadpoles can be distinguished from those of *M. zolitschka* by their external coloration and pattern and relevant differences in keratodont

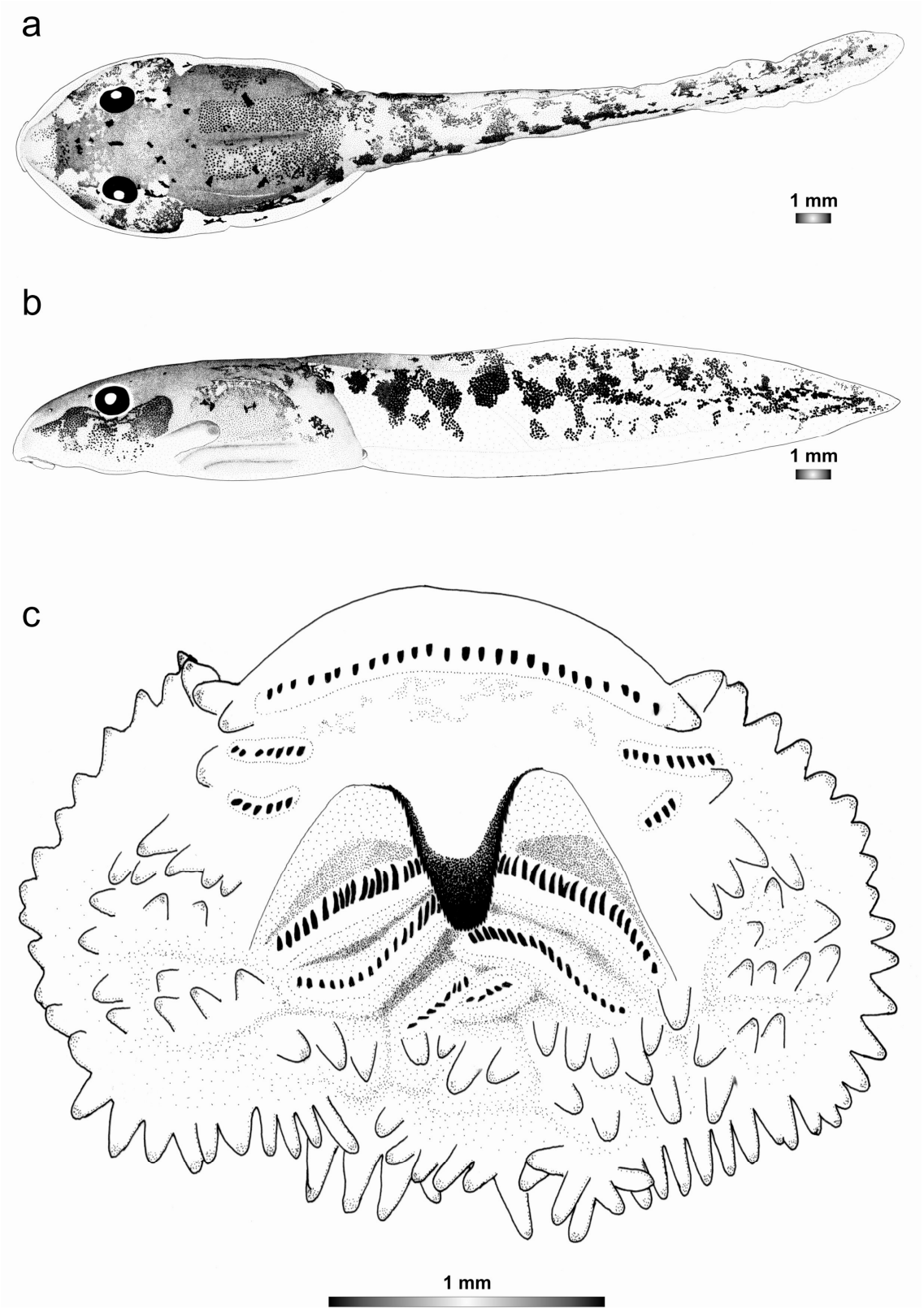

Figure 12. Drawings of the preserved DNA voucher tadpole of *Mantidactylus zolitschka* (ZCMV 3565-ZSM 1843/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

density and papillae number, but they have the same LTRF. *Mantidactylus* sp. 42 is also characterized by its keratodont rows which do not form a real chevron pattern as in other *femoralis*-like tadpoles.

Mantidactylus sp. 43

A species phylogenetically close to *M. mocquardi* but differing in its tadpole morphology. We found adult and larval specimens at lowland sites in the Marojejy massif, and similar to *M. mocquardi*, adults had conspicuous silvery color with a black pattern on the venter (Figure 2). The single tadpole assigned to this candidate species (ZSM 1610/2007-FGZC 2928, Gosner stage 25 from Marojejy National Park; see Figures 4 and 15) is easily distinguished from *M. femoralis*, *M. ambreensis*, *M. zolitschka* and *M.* sp. 42 tadpoles by its uniformly pale coloration in preservative (no data on life coloration is available). Dorsal surface of body and of tail muscle are flecked. Speckles are positioned in deep integumental layers, darker patches dissipate between eyes and along the vertebral area and brown spots disperse on dorsal and dorsolateral parts of body. The tail musculature has brown mottles which coalesce in some areas to form sparse reticulations. Fins are pale, with speckles especially on the proximal 1/4 of the dorsal fin. This tadpole is characterized by the scattered state of A_1, and its LTRF differs from those of *M. femoralis*, *M. zolitschka* and *M.* sp. 42 (but not from *M. ambreensis*) by having two instead of three upper rows of keratodonts. The presence of keratodonts makes it also easy to differentiate it from *M. mocquardi* (which lacks keratodonts).

Mantidactylus sp. 47

This confirmed candidate species is known from various sites in the Ranomafana region. Especially at Ambatolahy it is a very common species in a fast-flowing large stream where adult males and females are regularly found on large boulders next to the water. Females are much larger than males. In the adult stage, the ventral side is not conspicuously silvery, and there is no large and distinct yellow inguinal patch (Figure 2). The tadpole of *Mantidactylus* sp. 47 (based on ZSM 456/2008-ZCMV 2699, Gosner stage 31 from Ambatolahy next to Ranomafana National Park; see Figures 3, 4 and 16) has a small constriction anterior to the point where the maximal body width is attained. It shares the LTRF with *M. femoralis*, *M. zolitschka* and *M.* sp. 42 tadpoles (with three upper keratodont rows), but differs from *M. ambreensis* and *M.* sp. 43 (with only two upper rows). It can also be differentiated from the tadpoles of *M. femoralis*, *M. ambreensis* and *M.* sp. 42 by its variegated light brown coloration. It is characterized by the presence of slightly visible domino-like structure on the dorsum. In life, the body is covered by brown patches in deep

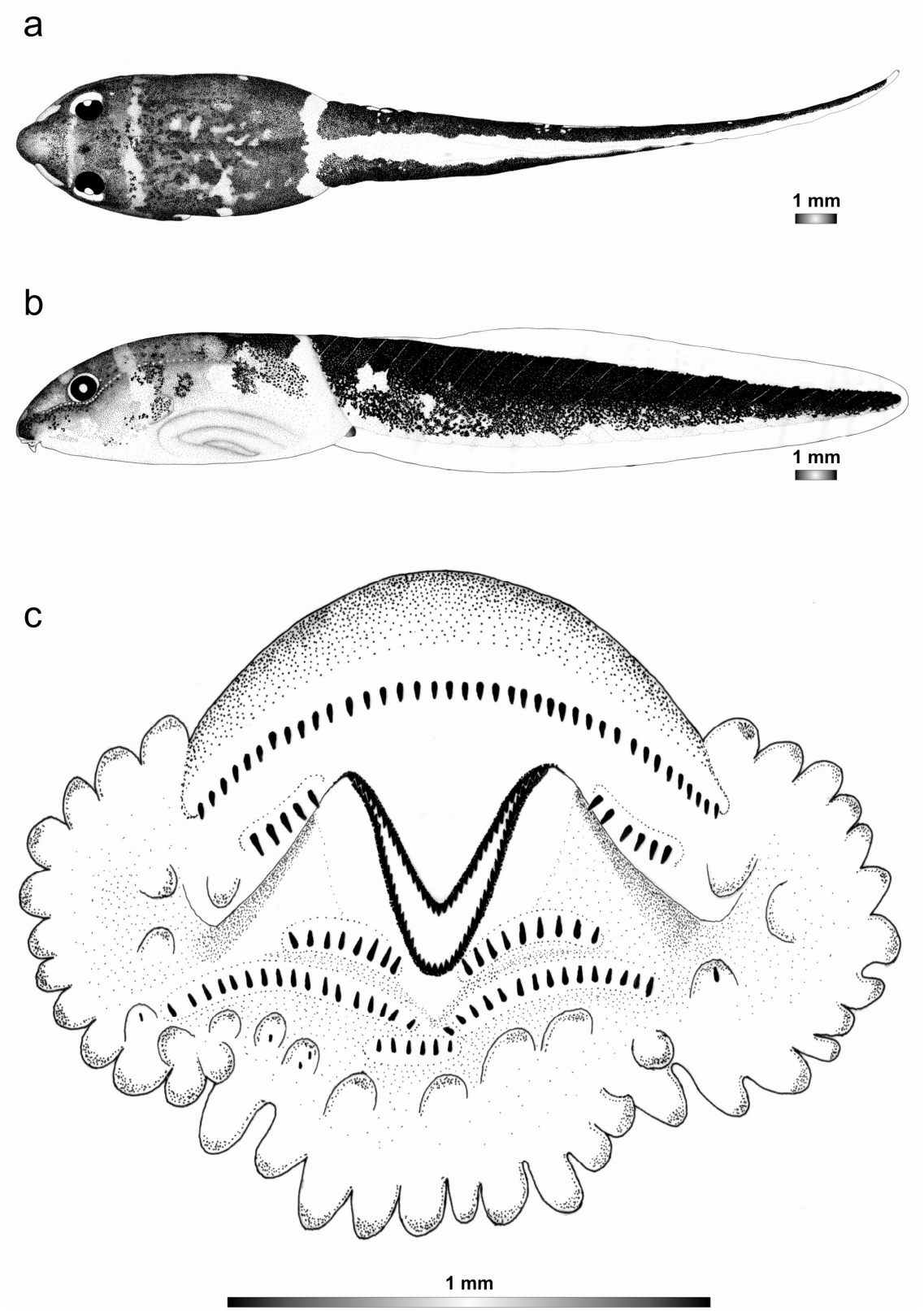

Figure 13. Drawings of the preserved DNA voucher tadpole of *Mantidactylus argenteus* (ZCMV 3575-ZSM 1573/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

integumental layers that are condensed especially between the eyes and on the vertebral region. Some dark brown and golden patches spread over the skin. Ventrally, gular region beige, branchial region reddish and abdominal surface transparent. Tail musculature beige with dark brown dots forming patches. Fins transparent, dorsal fin with many patches than the ventral fin. In preservative, it is largely brownish. Light brown pigment in deeper integument layers covers the dorsum and flanks of the body. Dark brown patches disperse on the skin. Brown spots coalesce to form networks which spread irregularly on the tail musculature. Fins are pale and the dorsal fin has some brown reticulations. Five additional DNA voucher specimens attributed to this species from the same locality and many additional specimens belonging to these series agree in most cases with the typical oral disk configuration (Figure 4) and the external pigmentation of this species. The LTRF shows some variation: 2(2)/3(1-2) and 3(2-3)/3(1-2).

Mantidactylus mocquardi

We consider as *M. mocquardi* a species characterized, in the adult stage, by a relatively large size, especially of some females, a somewhat tubercular dorsum, small and indistinct yellow inguinal patch, and distinct silvery belly (with or without black pattern; Figure 2). We confirm the taxonomic rationale of Glaw & Vences (2004) in assigning the nomen *mocquardi* to this species, because in the Northern Central East of Madagascar where the type locality of *M. mocquardi* is located, no other species except the one with silvery bellies was found which would be characterized by a large size of females and thus would morphologically conform with the *M. mocquardi* holotype (which is a large-sized female as well). Based on molecular data, we observed *M. mocquardi* at Ambohitsara, An'Ala, and Mahasoa forest.

The tadpole of *Mantidactylus mocquardi* (based on ZSM 1540/2007-ZCMV 3511, Gosner stage 25 from An'Ala; see Figures 4 and 17) is characterized by its light beige-brownish coloration in preservative, no data of the life coloration is available. Light brown blotches positioned in deep integumental layers form dark patches between nares and eyes and along the vertebral area and flank of the body. Some dark brown patches are scattered irregularly on the skin. The tail musculature is beige with a few patches which are dissipated irregularly. Fins are pale, with brown blotches in the dorsal fin. A reddish patch on the back of the nares is present. This tadpole has a very characteristic oral disk. It has a long narrowly pointed medial convexity, no keratodonts, a few short to moderately long and moderately large papillae, but no dorsal gap of marginal papillae (Figure 4). In comparison with the *femoralis*-like tadpoles, the main difference is the absence of keratodonts and the state of the papillae. Nine additional DNA voucher specimens from the same locality and one DNA voucher specimen from Ambohitsara-Tsitola assigned to this species show the same characteristic oral disk configuration and the same external pigmentation.

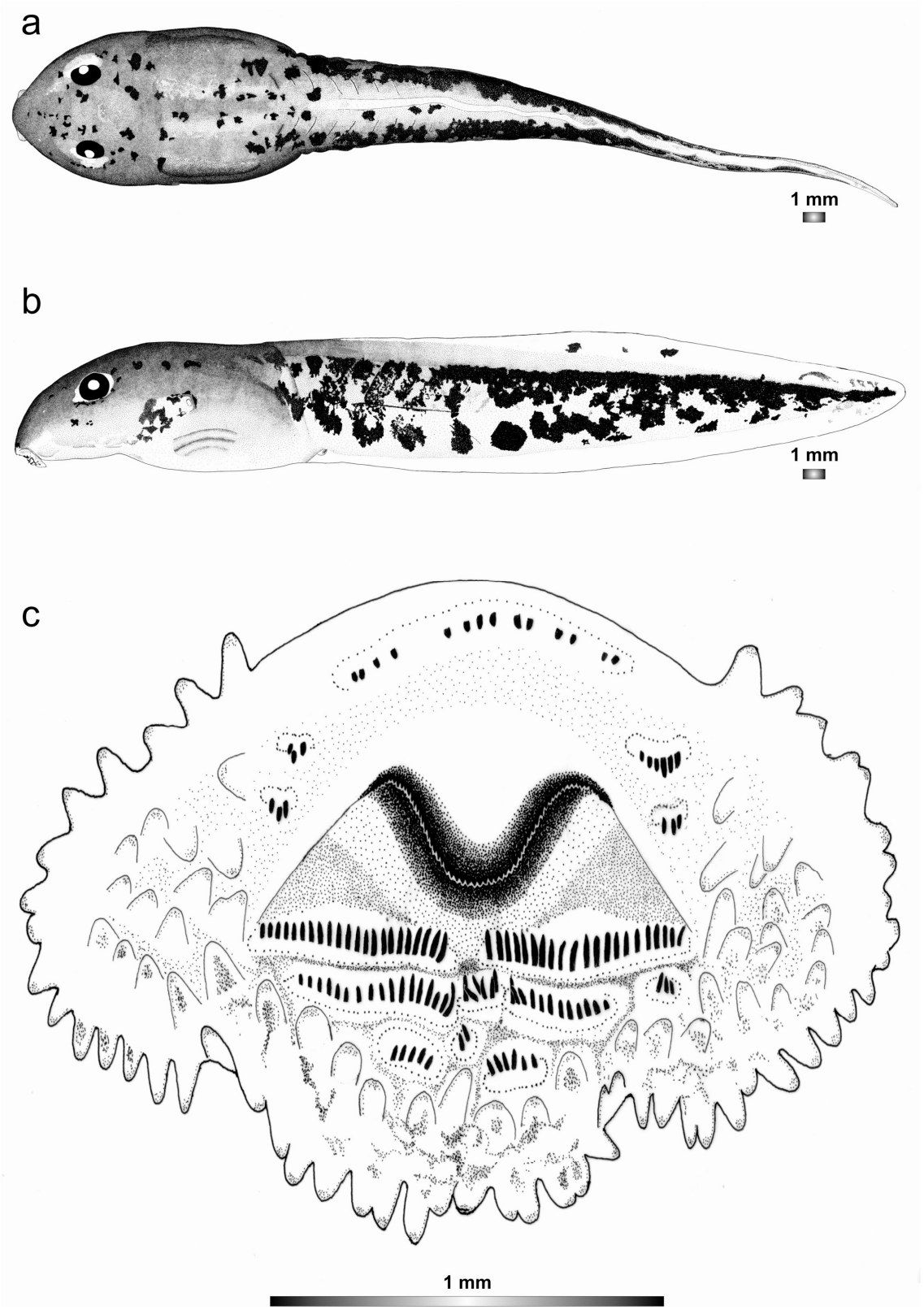

Figure 14. Drawings of the preserved DNA voucher tadpole of *Mantidactylus* sp. 42 (FG/MV 2002.1957-ZSM 774/2004): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

Tadpoles (ZSM 686/2008-ZCMV 8094; Figure 18) collected at Mahasoa forest differed by several external parameters but are here preliminarily assigned to *M. mocquardi* because genetically, this population is very similar to the other populations examined. The lack of keratodonts allows distinguishing these tadpoles from those of M. sp. 43 (the next closest relative of *M. mocquardi*). The tadpole has a rather large size in comparison to all other tadpoles studied, and a pale-brownish coloration in preservative (no data on life coloration is available). Light pale brown pigment covers the dorsum and is condensed especially behind the eyes, on the vertebral region and on the flank of the body. Some dark brown patches are scattered on the skin. The tail musculature has light brown speckles and dark brown spots which form patches. Fins are pale and the dorsal fin has brown spots which group to form patches. On the ventral fin, patches spread around tail tip. It has also the typical *M. mocquardi* oral disk. It furthermore is the only tadpole with a position of the maximal body height in the distal 1/4. Differences to *M. mocquardi* are in the shape of the snout in lateral view, the configuration and the form of the spiracle opening, the length of the tail, the origin of the dorsal fin, the location of the maximal tail height, the position and the direction of the oral disk, the low number of papillae, and the size of the medial convexity. Four additional specimens belonging to the same series (but not identified by DNA barcoding) have the same external morphology as the voucher specimen including oral disk configuration.

Mantidactylus sp. 64

This candidate species was first discovered by its deviant tadpole morphology, based on specimens from the Ranomafana area. So far, nothing is known about its adult morphology, although one adult has been collected at Vevembe (not available for morphological examination in the framework of this study). Based on mitochondrial DNA sequences this species appears to be closely related to M. sp. 47 (Figure 1). Its tadpole (based on ZSM 401/2008-ZCMV 2646, Gosner stage 39 from Ranomafana National Park (Figures 4, and 19) for the preserved tadpole and on ZCMV 9291 - not yet catalogued in ZSM (Figure 3) for the living tadpole) is characterized by its reddish-brown coloration in life. The body and the tail are covered by brown blotches which are condensed and give a dark brown coloration to the tadpole. Ventrally, gular region beige, branchial regions reddish, abdominal surface beige. In preservative, it is dark. Brown pigment covers the dorsum and flank of the body, and dark brown patches are scattered on the skin. The tail musculature is pale and covered by dark brown reticulations. Fins are pale and have brown reticulations close to the tail tip. This tadpole is similar to that of *M. mocquardi* (and differs from the *femoralis*-like tadpoles) by the configuration of its oral disk, *i.e.*, absence of keratodonts and of a dorsal gap of marginal papillae. However, the pigmented and moderately wide oral disk with

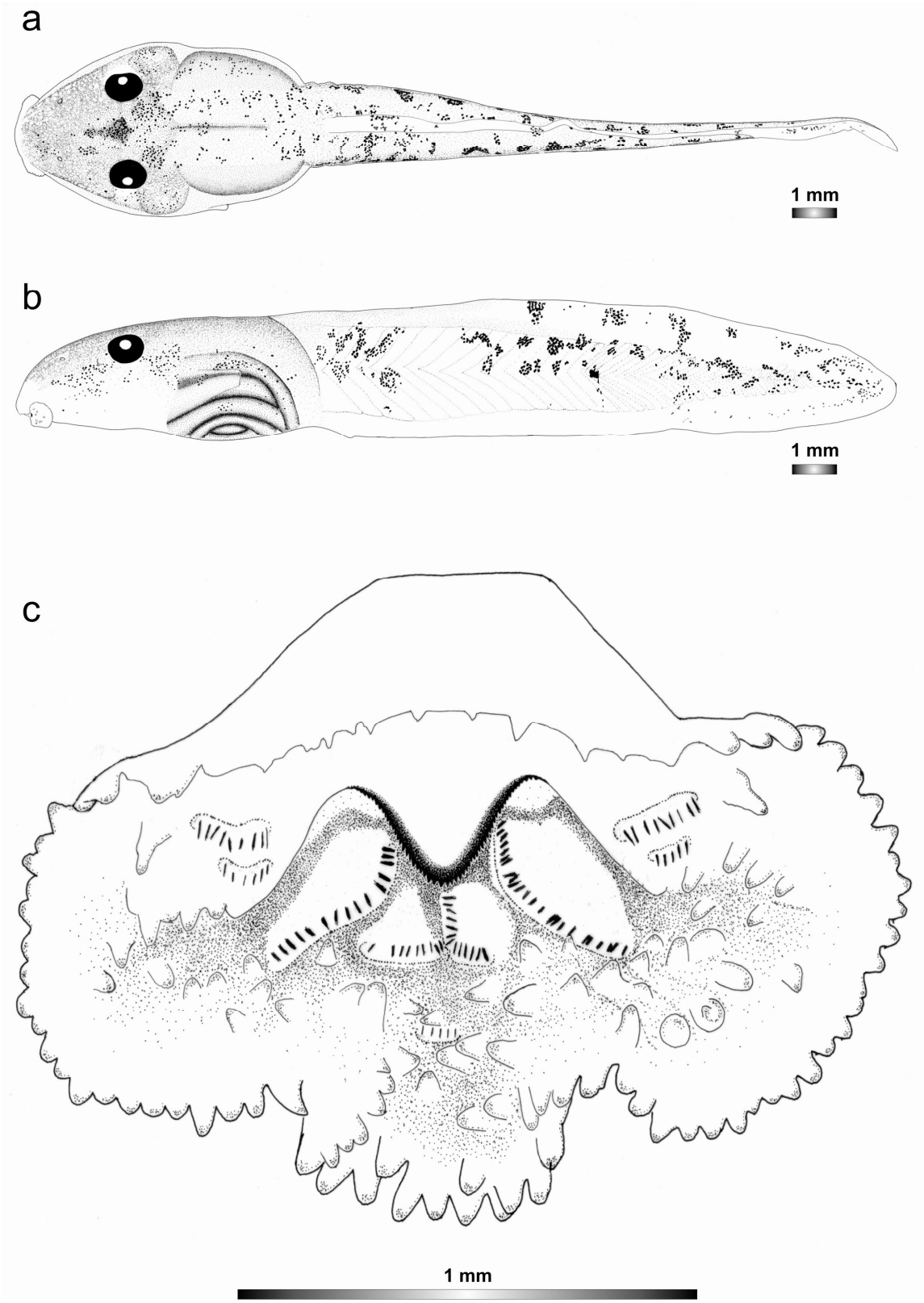

Figure 15. Drawings of the preserved DNA voucher tadpole of *Mantidactylus* sp. 43 (FGZC 2928-ZSM 1610/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

rather small and short conical papillae is unique to this species. There are further morphological differences to *M. mocquardi*, like the uniformly dark coloration that the tadpoles of this species have. In lateral view, the snout is narrowly rounded (broadly rounded in *M. mocquardi*). The eyes are situated between the proximal 2/10 and 3/10 of the body (*vs.* between the proximal 3/10 and 4/10 in *M. mocquardi*). The vent tube is moderately long, the tail is long, tail musculature is moderately developed and the tail tip is narrowly rounded, and the medial convexity is short and widely rounded (*vs.* short vent tube, short tail, developed tail musculature and pointed tail tip, and long and narrowly pointed medial convexity in *M. mocquardi*). The dorsal fin originates at the proximal 1/10 of the caudal musculature (*vs.* on the dorsal body-tail junction in *M. mocquardi*). One further uncataloged DNA voucher specimen (ZCMV 9291) from Sakaroa in Ranomafana National Park attributed to this species displays the same external pigmentation in preservative. A more detailed examination of its oral disk was not possible because the specimen was not available for further examination.

Mantidactylus majori

This species is in its adult phase easily recognizable by the rather uniform light brown dorsal coloration bordering at the flanks rather sharply to the white venter, absence of a yellow inguinal patch, a smooth dorsum, and a pointed snout (Figure 2). The species is common in the Southern Central East and South East; based on molecular identification, we confirm its occurrence in the Ranomafana region, Vevembe, and Midongy du Sud; recently, it has also been found in Sahafina in the Northern Central East (Gehring et al. 2010). As reported by Lehtinen (2003), Vences & De la Riva (2005), and Altig (2008), this species deposits eggs on leaves overhanging streams, guarded by the male. We confirm this reproductive mode by molecular identification of clutches, and also confirm that in these clutches, small tadpoles develop which eventually drop into the stream (Figure 5). The tadpoles of *M. majori* (based on ZSM 1684/2007-ZCMV 3762 Gosner stage 29 and T 09/746 Gosner stage 25 from Ranomafana National Park; see Figures 3, 4, and 20) have the most derived oral disk among *Ochthomantis*, lacking all keratinized components (keratodonts and jaw sheath). The upper jaw sheath is transformed into three very large flexible, slightly curved and thorn-shaped projections and a dozen of large papillae are situated near the base of what appears to be a non-pigmented, non-keratinized, non-serrated lower jaw sheath that is totally hidden by the upper jaw sheath (Figure 4).

In life, coloration of these tadpoles is beige-orange with brown patches. Light brown patches are positioned in deep integumental layers are between the eyes and on the vertebral region. Dark brown and golden patches spread over the skin. Ventrally, gular region beige, branchial region reddish, abdominal surface transparent with golden patches, intestinal coil

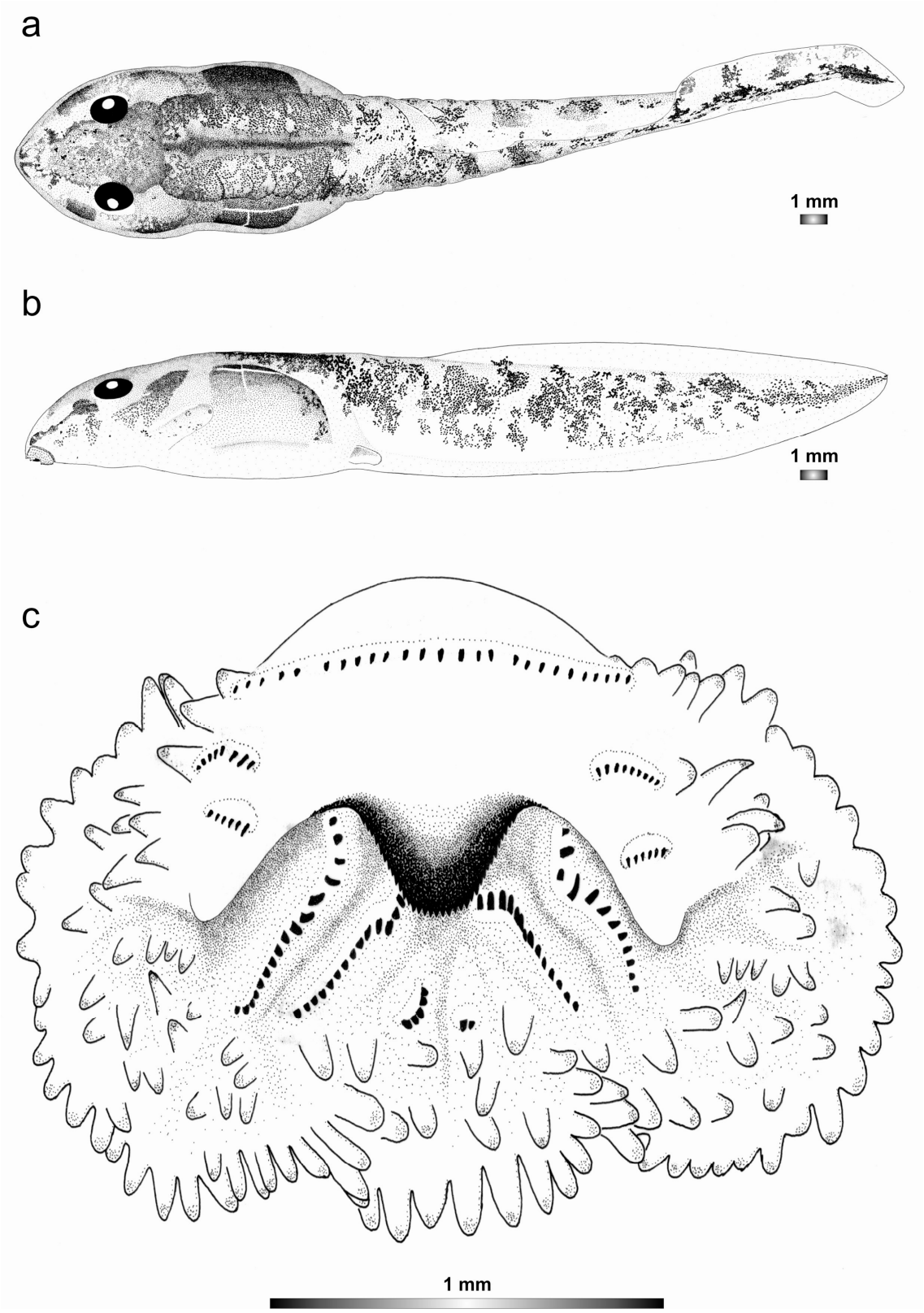

Figure 16. Drawings of the preserved DNA voucher tadpole of *Mantidactylus* sp. 47 (ZCMV 2699-ZSM 456/2008): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

visible with regular spiral-shaped intestine. Tail musculature is orange-yellowish with light brown dots arranged in patches. Fins are transparent. The dorsal fin has more patches than the ventral fin.

In preservative, coloration is generally yellowish with brown patches between the eyes and the nares that are positioned in deep integumental layers. Light brown patches disperse on the dorsum and the upper part of the flank and dark brown blotches dissipate on the dorsum and the flank. Tail musculature is pale with light brown dots that fuse in some areas and form patches towards the tail tip. Fins are transparent, the dorsal fin and the distal part of the ventral fin have the same coloration as the tail muscle. The external morphology of this tadpole differs from that of the *M. mocquardi* tadpole by the remarkable ovoid body form in dorsal view, the lateral eye direction, the wide distance between the eyes, the moderately sized and the elliptical shape of the opening of the nares, the moderately wide distance between the nares, the configuration of the spiracle opening, the size of the vent tube and the tail, the origin of the dorsal fin, and the shape of the tail tip. Thirty-two additional DNA voucher specimens from the same locality and one voucher specimen from Vevembe forest attributed to this species reveal the same characteristic oral disk configuration, the external pigmentation, and all other morphological characteristics of this species.

Three further candidate species of the subgenus *Ochthomantis* are only known from adults so far and are here considered as UCS: *Mantidactylus* sp. 61 from Andapa is known to us from a single specimen with a distinct frenal stripe, smooth dorsal skin and a rather pointed head. *Mantidactylus* sp. 62 from higher elevations of the Marojejy massif (ca. 1100 m a.s.l., at a site locally known as Camp Simpona) is a rather characteristic species with smooth skin, large-sized females, and a more or less uniform beige venter without white-silvery color. *Mantidactylus* sp. 63 from the Tsaratanana and Manongarivo massifs in the Sambirano region is a relatively large species with a discontinuous yellowish lateral line bordered dorsally by areas of black skin, and with a venter with yellow color and a distinct pattern of black spots.

2. Ecological analysis

In Ranomafana National Park, during the rainy season, tadpoles of 44 species were found in streams including four species of the subgenus *Ochthomantis*: *Mantidactylus femoralis*, *M. majori*, M. sp. 47 and M. sp. 64. *Ochthomantis* tadpoles were found in 20 out of 33 streams, and often tadpoles of different species occurred together in the same streams. They were never the most abundant species but three of the species represented in some streams a considerable proportion of the overall number of tadpole specimens collected. *Mantidactylus femoralis* occurred in seven

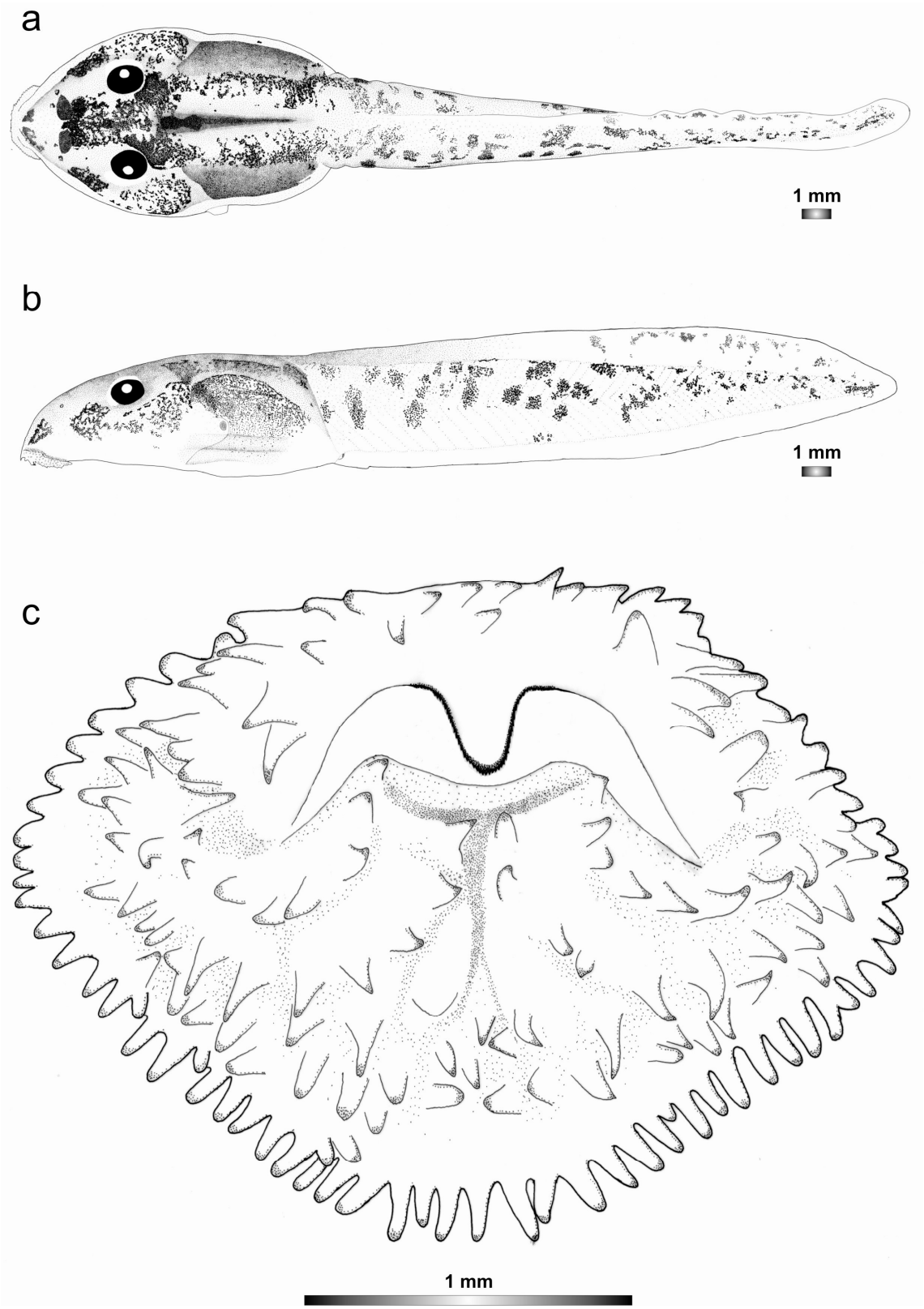

Figure 17. Drawings of the preserved DNA voucher tadpole of *Mantidactylus mocquardi* (ZCMV 3511-ZSM 1540/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

streams with a mean of five specimens per 30 m sample transect (range: 1 to 13 specimens), *M. majori* occurred in eleven streams with a mean of 16 specimens (1 to 68), and M. sp. 47 occurred in 16 streams with a mean of 6 specimens (1 to 25), M. sp. 64 was only found with a single specimen at one stream. For *M. majori*, several observations on clutches and embryonal development were made (Fig. 5). One clutch with about 40 embryos was found attached to a leaf 40 cm above a stream. Further two clutches with already well developed tadpoles were found attached to a branch of a shrub and attached to a *Pandanus* leaf, respectively, both about 1.2 m above another stream. Tadpoles were hatching from the jelly immediately after induced vibrations. An adult *M. majori* male was observed guarding an egg clutch that was attached to a leaf 80 cm above a stream.

During the dry season, congruent with the generally low number of tadpole specimens of mantellid species in this area and season, *Ochthomantis* tadpoles were present but in only very low numbers. Out of 13 sampled streams, *Mantidactylus femoralis* occurred in one stream with two specimens, *M. majori* occurred in three streams with a mean of nine specimens per 30 m transect (range: 2 to 20 specimens), and M. sp. 47 occurred in five streams with a mean of four specimens (1 to 9). No tadpoles of M. sp. 64 were found in the dry season; however, none of the streams where they have been observed before were sampled. In four streams, tadpoles of two *Ochthomantis* species (*M. femoralis* and M. sp. 47) were observed in the dry but not in the rainy season.

In our statistical analyses of habitat choice (Figure 6 and 8) we first compared breeding site choice of *Ochthomantis* species on the spatial level of Ranomafana NP, *i.e.*, the distribution of tadpoles between 33 different streams, applying data ordination (principal component analysis; PCA) and subsequently including the PC factors as independent variables in a generalized linear model (GLM). PCA on the original habitat (stream) variables and the surrounding forest resulted in three PCs, explaining together 67.6% of the variation in the data. Based on the loadings of the PCs and the results of the bootstrapped-eigenvector method (Peres-Neto et al. 2003) we identified the following habitat variables being well represented ('+' positive correlation, '−' negative correlation): PC1 (33.9%) slope (+), canopy cover of forest (+) and stream (+), overhanging vegetation (+), width (−) and depth (−) of the stream. The variables that contributed the most to PC2 (18.0%) were slope of the stream (+), the number of shrubs in the forest (+), number of trees (−) and leaf litter depth (−) in the forest. The number of small trees and shrubs in the forest (+) and overhanging vegetation (+) contributed to PC3 (15.7%). However, according to bootstrapped-eigenvector method both PC2 and PC3 do not well represent the above mentioned habitat variables.

The presence or absence of *Ochthomantis* tadpoles was negatively correlated with PC1 (Figure 6; GLM with binomial error distribution; residual deviance=26.6 on 31df, p=0.009), all

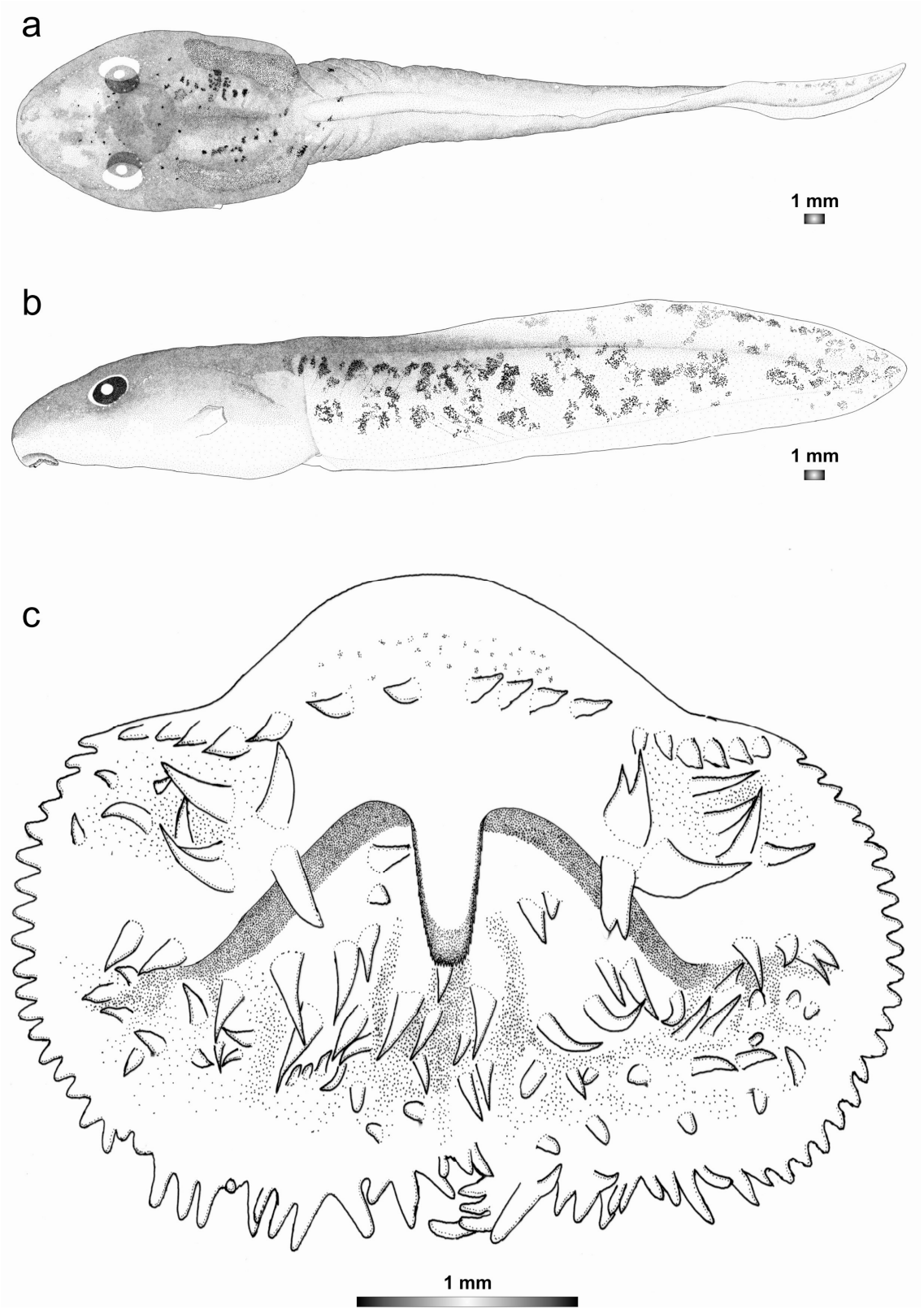

Figure 18. Drawings of the preserved DNA voucher tadpole of *Mantidactylus mocquardi* from Mahasoa (ZCMV 8094-ZSM 686/2008): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

other PCs as well as interactions could be removed from the model. Therefore, *Ochthomantis* species prefer larger streams with an open canopy directly at the stream and also a relatively open canopy in the surrounding forest, and with a gentle slope (*i.e.*, slow running streams; see also Figure 8). Second, we compared microhabitat choice of *Ochthomantis* species on the spatial level of each stream, *i.e.*, the distribution of tadpoles within each stream.

The tadpoles were not found in all microhabitats that were available in the streams. Most of the specimens were found in those areas of a stream with leaves or sand as substrate combined with slow moving to almost stagnant water (Figure 7a). In detail, *Ochthomantis* tadpoles avoided most microhabitats including all microhabitats in fast moving water ($E<0$; factorial ANOVA, $F_{7,233}=26.93$, fast rock ($E=-1\pm0.14$; mean ± SE), fast gravel ($E=-0.95\pm0.096$), fast sand ($E=-0.87\pm0.13$), fast leaves ($E=-0.77\pm0.13$), slow rock ($E=-0.79\pm0.14$) and slow gravel ($E=-1\pm0.15$, p always <0.001) (Fig. 7B). We also detected a non-significant trend of avoidance for the microhabitat slow sand ($E=-0.17\pm0.09$, $p=0.063$). Slow leaves was the only microhabitat significantly preferred by *Ochthomantis* tadpoles ($E>0$; factorial ANOVA, $E=0.33\pm0.09$, $p<0.001$). It needs to be noted, however, that the general strong avoidance values can partly be caused by a high number of non-occurrence events in the specific microhabitats in some streams. As all microhabitat-species interactions could be removed from the model, our data do not show significant differences in the choice of microhabitat for the three most abundant *Ochthomantis* species. Due to their low abundance, no index of preference was calculated for *M.* sp. 64 tadpole. However, the few specimens were exclusively found in slow leaves microhabitat.

Discussion

1. Specialization of the oral disk in *Ochthomantis* tadpoles

Ochthomantis tadpoles have morphological characters showing a high degree of specialization, which are *(1)* reduction and *(2)* change in the components of the oral disk. Because of the character reduction seen in some species, the states of many characters cannot be assessed which makes some inter-species comparisons difficult. The general external morphology of these tadpoles shows no large differentiation. They are in general tadpoles with a rather low dorsal fin and were all collected in flowing waters. Only few external characters other than the mouthparts show differences among species, such as the position of the spiracle and the color.

Summarizing the most relevant variation, it is possible to distinguish three main morphological clusters of *Ochthomantis* tadpoles that probably represent different evolutionary steps of reduction and change in the oral disk:

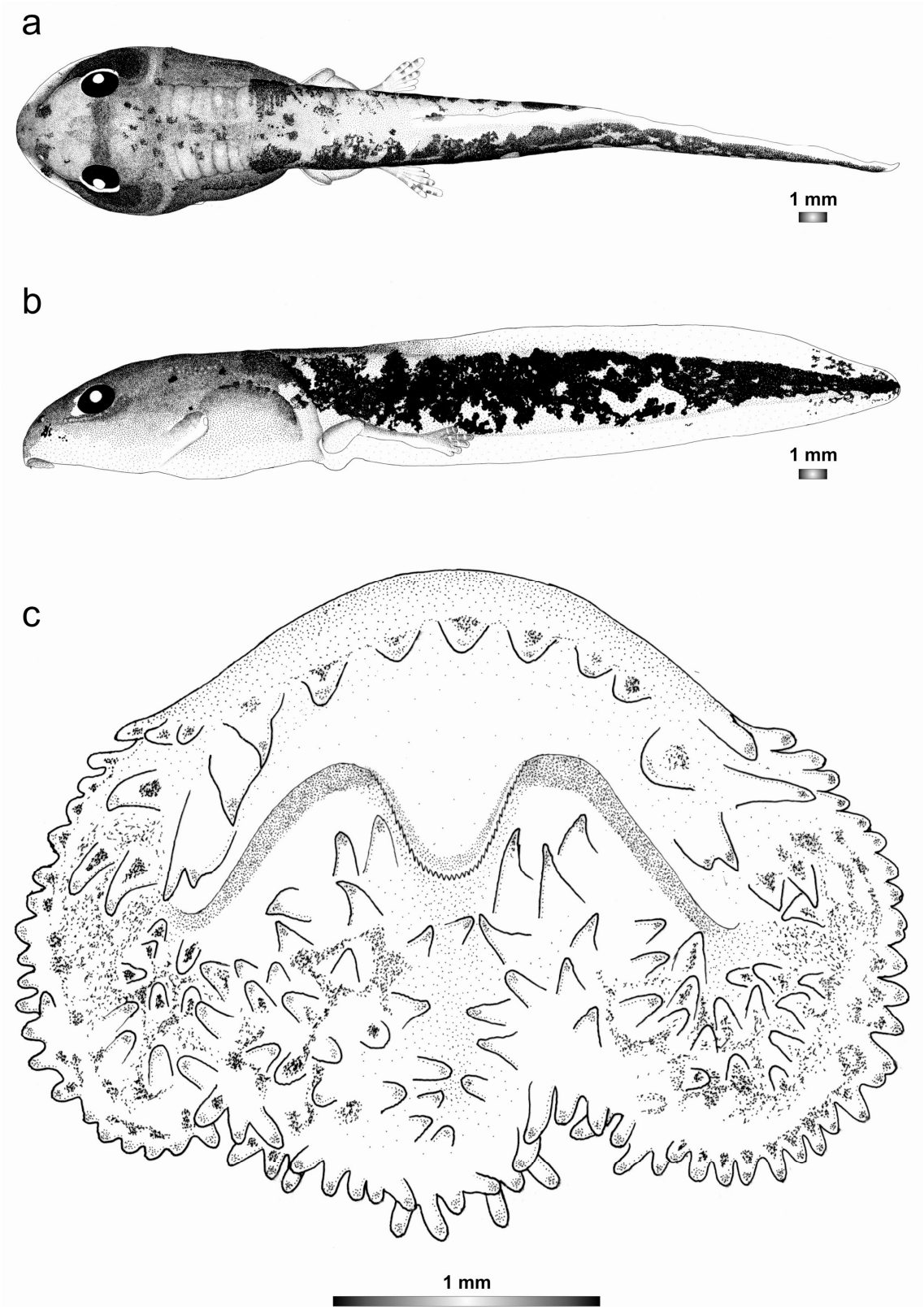

Figure 19. Drawings of the preserved DNA voucher tadpole of *Mantidactylus* sp. 64 (ZCMV 2646-ZSM 401/2008): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

(1) Mantidactylus femoralis, *M. ambreensis*, *M. zolitschka*, M. sp. 42, M. sp. 43 and M. sp. 47 possess reduced jaw sheaths and keratodonts. Summarizing morphological characters, these tadpoles are characterized by a small to moderately wide oral disk (ODW 32 to 47% of BW), moderately wide and poorly keratinized jaw sheaths (JW 35 to 54% of ODW), an upper jaw sheath having a short to long, narrowly to widely, pointed or rounded medial convexity (MCL 17 to 31% of JW) and many finely pointed serrations, a lower jaw sheath totally hidden by the upper ones, very few (MP 31 to 71, SMP 18 to 59) short (MP 0.08 to 0.12 mm, SMP 0.08 to 0.20 mm) and moderately large conical papillae with rounded tips, a moderately wide dorsal gap of papillae (DG 45 to 66% of ODW), an absence of ventral gap of papillae, a LTRF of 2(2)/3(1-2) or 3(2-3)/3(1-2), small keratodonts (0.04 to 0.09 mm), lower keratodont rows forming a chevron and P_2 and P_3 are usually scattered, a wide A_2 gap (61 to 82% of A_2). All of these tadpoles show what we interpret as the first step of reduction of keratinized structures, namely *(1)* the jaw sheath is not fully keratinized (*i.e.*, only at the edge) and has a medial convexity, and *(2)* there are only few upper keratodont rows (usually three, further reduced to only two in *M. ambreensis* and M. sp. 43), there are only relatively low numbers of keratodonts per row, the second lower tooth row is interrupted (uninterrupted in generalized mantellid tadpoles), and all lower rows are scattered and form a chevron. In addition, *M. zolitschka* shows a reduction of the keratinization of the keratodonts which become difficult to recognize without using a staining agent such as methylene blue. Also M. sp. 43 has reduced the keratodonts on A_1.

(2) The second group contains *M. mocquardi* and M. sp. 64. These tadpoles are characterized by a small to moderately wide oral disk (ODW 34 to 47% of BW), moderately wide and poorly keratinized jaw sheaths (JW 32 to 55% of ODW), an upper jaw sheath having a long to very long narrowly pointed medial convexity (MCL 21to 57% of JW) and many finely pointed serrations, a lower jaw sheath totally hidden by the upper ones, few (MP 64 to 89, SMP 77 to 104) and very short to long (MP 0.09 to 0.25 mm, SMP 0.12 to 0.35 mm) and large conical to elongated papillae with rounded (MP) and pointed (SMP) tips, an absence of dorsal and ventral gaps of papillae, and an absence of keratodonts (LTRF 0/0). In terms of reduction of keratinized structures, the jaw sheaths in these species have the same state as found in the first morphological group but the keratodonts are completely reduced and many submarginal papillae are present in the area occupied by keratodont rows in the other species. The row of marginal papillae is complete (*i.e.*, there is no dorsal gap). These tadpoles have long and moderately large elongated papillae, mainly in *M. mocquardi* from Mahasoa whose submarginal papillae show similarities to those of *M. majori*.

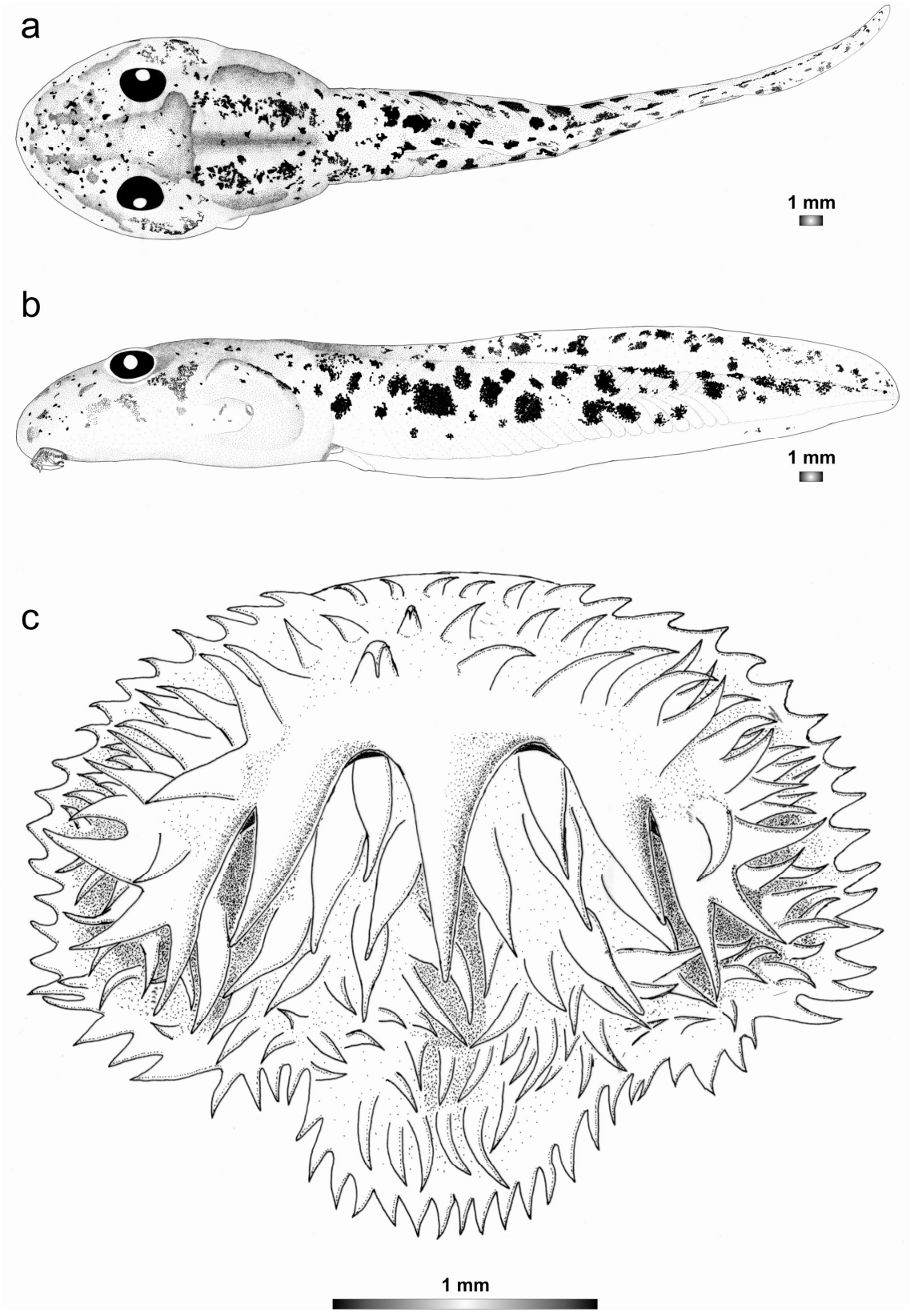

Figure 20. Drawings of the preserved DNA voucher tadpole of *Mantidactylus majori* (ZCMV 3762-ZSM 1684/2007): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

(3) The third group only contains the highly modified tadpoles of *M. majori* which are characterized by a small oral disk (ODW 38 to 40% of BW), an upper jaw sheath transformed into three thorn-shaped papillae (projections), a lower jaw sheath totally hidden by the upper ones, moderately many (MP 72 to 105, SMP 135 to 201) long to very long (MP 0.22 to 0.25 mm, SMP 0.41 to 0.52 mm) and very large elongated papillae with pointed tips, an absence of dorsal and ventral gaps of papillae, an absence of keratodonts (LTRF 0/0). The modification of the area of the jaw sheaths in this species is extreme and besides the three very large flexible slightly curved thorn-shaped papilla-like structures there are some large elongated papillae projecting from near the base of what appears to be a non-pigmented, non-keratinized, non-serrated lower jaw sheath.

The phylogenetic tree shown here (Figure 1) needs to be considered as tentative because it is based on a rather short fragment of only one mitochondrial gene. We therefore refrain from a detailed discussion here but just mention some aspects that seem to be well supported (Bayesian posterior probabilities of >0.95). However, the phylogenetic relationships proposed in this tree are in need of further confirmation by a forthcoming multi-gene analysis. First, it seems clear that *M. majori* is the most divergent *Ochthomantis* and may even be more distant to other *Ochthomantis* than is *Mantidactylus* (*Maitsomantis*) *argenteus*. This could indicate that the reduction of keratinized oral structures in *M. majori* occurred convergently to what is observed in the *M. mocquardi*-like species. Second, it seems clear that *Ochthomantis* cannot be simply divided into two clades, one with a *M. femoralis*-like tadpole morphology and one with a (more specialized) *M. mocquardi*-like morphology. This situation is exemplified by the clade containing *M. mocquardi* and *M.* sp. 43 on one hand, and the clade containing *M.* sp. 47 and *M.* sp. 64 (which however is not strongly supported) on the other hand: In fact, *M. mocquardi* and *M.* sp. 64 show a full loss of keratodonts which is not shown by their respective sister taxa (*M.* sp. 43 and *M.* sp. 47), indicating that this loss may have occurred convergently in the two lineages. The tendency of keratodont loss on A_1 of *M.* sp. 43 nevertheless indicates an early tendency of loss of keratodonts in this lineage.

2. Comparisons with other mantellid tadpoles

A convergence in the reduction of the oral disk in mantellid tadpoles is found between the subgenus *Ochthomantis* and the genus *Boophis* (*B. majori*; Schmidt et al. 2008, and pers. obs.). *Boophis majori* tadpoles have a small oral disk, a poorly keratinized jaw sheath with a very long narrowly pointed medial convexity and finely pointed serrations, a wide dorsal gap of marginal papillae an absent ventral gap of papillae. The difference is that *B. majori* tadpoles do not possess any conspicuous modifications of the keratodonts. They have one interrupted lower row as it is typical for many *Boophis* tadpoles, and their LTRF are 4(2-4)/3(1) (Schmidt et al. 2008, pers. obs.)

and 5(2-5)/3(1) (pers. obs.). The tadpoles of *B. picturatus* (Altig & McDiarmid, 2006; pers. obs. of many DNA voucher specimens from Ranomafana National Park) show the most extreme evolutionary specialization in having an extraordinary reduction of various oral disk characters.

Mantidactylus argenteus is classified in the subgenus *Maitsomantis* because of its largely arboreal habits in the adult stage which is unique in *Mantidactylus* (Glaw & Vences, 2006). Its tadpoles are easy to recognize because of the bands on the body, but the oral disk is *femoralis*-like with a LTRF of 2(2)/3(1-2) (see Figure 4). This would imply that the ancestor of *Maitsomantis* and *Ochthomantis* probably had *femoralis*-like tadpole features. There is a further tendency of specialization in the mouthparts of the *mocquardi*-like lineage. According to the molecular tree presented here, the subgenus *Ochthomantis* would be paraphyletic, with *M. majori* being sister to a clade of all other *Ochthomantis* plus *M. (Maitsomantis) argenteus*. However, because this tree is based on only few sequences, we consider this grouping as in need of confirmation. So far, no comprehensive phylogenetic analysis of morphological character states of mantellid tadpoles have been published, but an own study in progress indicates that various of the states of *Ochthomantis* and *Maitsomantis* (*e.g.*, the reduction of keratodont rows) are derived, indicating that tadpole characters may provide support for their phylogenetic relationships. A further derived character state shared by *M. majori* and *M. argenteus* is the male egg-guarding of eggs deposited on leaves overhanging running water (Vences & De la Riva 2005; Glaw & Vences 2007; Altig 2008). Vejarano et al. (2006) reported the presence of three interrupted lower rows (2(2)/3(1-3)) in *M. argenteus* tadpoles, but based on our data presented herein, we assume that it normally has only two interrupted lower rows, *i.e.*, an LTRF of 2(2)/3(1-2) (as indicated by the intact state of P_3 of the specimens examined herein; Figure 4). The data of Vejarano et al. (2006) might be due to the fact that the lower rows, mainly the third, are scattered in *M. argenteus*, similar to the situation in all *femoralis*-like tadpoles. Taking into account that *M. argenteus* tadpoles still have an uninterrupted third lower row agrees with the state in the first group of *Ochthomantis* tadpoles.

Previous descriptions of tadpoles of *Ochthomantis* have not been based on DNA barcoding, and given the high similarity among adults, species identification in these previous works is doubtful. Blommers-Schlösser (1979 in her Figures 9 and 10) provides a brief description of a tadpole assigned to be *M. femoralis* which shows scattered keratodonts on P_2. The tadpole has poorly keratinized jaw sheaths which are typical in *Ochthomantis*, but the combination of having both complete marginal papillae rows and keratodonts does not fit any *femoralis*-like tadpoles, since according to our observations only the tadpoles which have no keradotonts present no dorsal gap of marginal papillae (*mocquardi*-like tadpoles). Also, the LTRF 0/2+2 does not correspond with any *femoralis*-like nor *mocquardi*-like tadpoles. Maybe this is due to the captive

rearing of the tadpoles by Blommers-Schlösser (1979), or an artefact in the observation, or these tadpoles belong to yet another *Ochthomantis* candidate species that is not present in our samples.

Altig & McDiarmid (2006) described a tadpole from Ranomafana with strongly reduced keratinized structures in the oral disk and assigned it tentatively to *Mantidactylus guttulatus*, the largest mantellid frog whose life history is so far largely unknown. However, a comparison of the description and drawing with our study leaves little doubts that the authors in fact described the tadpole of *M. majori*. Altig & McDiamid (2006) had based their tentative identification on the morphology of juveniles which however can be very similar among *M. majori* and *M. guttulatus*.

3. Habitat selection and ecology of *Ochthomantis* tadpoles

Ochthomantis tadpoles are almost omnipresent in stream communities in the mid-elevational rainforests of Madagascar. Some *Ochthomantis* species can be found in many streams with considerable abundances, however, by far they do not represent the most common species (own unpublished data). *Ochthomantis* tadpoles occur throughout the year but with a strongly reduced abundance in the dry season. As all streams sampled were permanently water-bearing the reduced abundance may be caused by the low temperature, which is a main factor for frog reproduction in RNP (Andreone 1996). The presence of *Ochthomantis* species in four streams in the dry season where this species was not found in the preceeding rainy season indicates that reproduction occurs throughout the year.

Ochthomantis tadpoles avoid small, fast running streams surrounded by dense vegetation for reproduction. This may partly conflict with the fact that adults of at least *M. majori* attach eggs on vegetation above the water. However, these structures are obviously not a limiting resource even in the larger streams. A dense vegetation above the stream, here measured as overhanging vegetation and canopy cover, may cause decreasing light, lower dissolved oxygen, reduced temperature and reduced availability of food for tadpoles in ponds (Werner & Glennemeier, 1999) and influence periphyton growth and thus food availability in streams (Altig et al. 2007; Mallory & Richardson 2005). However, given that *Ochthomantis* tadpoles most probably live and feed among dead leaves on the ground of the streams, it is unlikely that periphyton growth would have strong influences on the amount of food available to them. Since the adults of *Ochthomantis* typically are found along or at few meters distance from the streams, dense vegetation along the streams might influence adults rather than tadpoles. Testing this hypothesis would require an analysis of the habitat preferences of adult *Ochthomantis* which so far has not been carried out.

Within a stream, *Ochthomantis* tadpoles of the three most abundant species do not obviously differ in their choice of microhabitat based on the rather rough microhabitat categories

distinguished in our sampling scheme. They prefer those areas of a stream with a slow current and an abundance of leaf litter. The same microhabitat preference was observed for tadpoles in the *Mantidactylus* subgenus *Chonomantis* (Grosjean et al. 2011). In general, microhabitat choice of tadpoles can be related to oral disk characteristics and therefore feeding mode (Altig & Johnston 1989). The fact that these morphologically very different tadpoles (*i.e.*, *Chonomantis* have funnel-shaped oral disks) show a similar habitat choice indicates that this might be a general pattern for most mantellid stream tadpole species that have no obvious adaptations to strong water currents (like *e.g.*, some *Boophis*, Glos et al.2007). As all other substrates in the slow running areas of the streams have been avoided, the strength of the water current may be only one important factor for microhabitat choice. It is therefore the combination of low water current and the high availability of nutrients within the leaf litter that is of importance for the preference for this microhabitat.

However, because *Ochthomantis* tadpoles occurring in Ranomafana show distinct tadpole morphologies and that some of them have unique oral disks (especially those of *M. majori*) it is unlikely that all of them use precisely the same food resources, despite a general agreement in rough microhabitat categories. Certainly, the species with the most derived oral disks (the second and third guild as defined above), without keratodonts and partly with modified jaw sheaths, are not able any more to graze and scrape as generalized tadpoles do, but it is uncertain whether tadpoles of the first group might show such a behavior or feed differently.

Although larvae of *Ochthomantis* and *Chonomantis* also share a similar choice of rough microhabitat categories (Grosjean et al. 2011) it is almost certain that these taxa will not use the same nutrient resources. Their very different and specialized oral disk structures strongly suggest different feeding behavior, *e.g.*, *Chonomantis* tadpoles may feed at least partly from the water surface as is known from other funnel-mouthed tadpoles (Grosjean et al. 2011), so that competition for food is not necessarily to be expected. In general, the high amount of morphological larval variation among *Ochthomantis* tadpoles stands in stark contrast to the situation in *Chonomantis* which show a very limited morphological differentiation although up to five *Chonomantis* species have been detected syntopically (Grosjean *et al.* 2011).

Tadpoles of the different species of *Ochthomantis* (and *Chonomantis*) often occurred together in the same stream, which demonstrates that they are not excluding each other and indicates that direct competition might be of minor importance. We assume that rather habitat characteristics and drift events determine the presence, abundance or absence of a species in a stream. Further insights into resource partitioning among these tadpoles will require detailed behavioral and ecological studies focusing on intestine contents, feeding behavior and feeding microhabitat, and activity periods.

Applying the definitions of ecomorphological tadpole guilds proposed by Altig and Johnston (1989) is generally difficult in Malagasy tadpoles because of the lack or different

expression of some of the characters that these authors have used (Randrianiaina et al. 2009a). Therefore, none of the guilds defined by these authors, nor the ones defined by Raharivololoniana et al. (2006) for *Boophis* tadpoles, are fully applicable to tadpoles of *Ochthomantis*. Based on our assumption that the different morphologies of the oral disk might correspond to the use of different nutrient resources, the three morphological clusters of *Ochthomantis* tadpoles defined above might in the future be considered as three ecomorphological guilds. However, such definitions will make more sense if proposed in the context of a future more comprehensive analysis of the morphology of mantellid tadpoles.

'Reverse taxonomy', *i.e.*, the initial survey of the diversity of a group of organisms via DNA barcoding only, has been introduced for cases where taxon diversity cannot be handled with traditional approaches (Markmann & Tautz 2005). Although such cases will usually refer to groups of insufficiently assessed taxa such as meiobenthos or nematodes (Blaxter 2004; Markmann & Tautz 2005), our example shows that it may also be fruitful in generally better studied groups such as vertebrates.

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Chapter 5

Nidicolous tadpoles rather than direct development in Malagasy frogs of the genus *Gephyromantis*.

This chapter is revised in Journal of Natural History as follows:

Randrianiaina RD, Wollenberg KC, Rasolonjatovo HT, Strauß A, Glos J, Vences M. 2001. Nidicolous tadpoles rather than direct development in Malagasy frogs of the genus *Gephyromantis*. Journal of Natural History.

Abstract

Frogs in the genus *Gephyromantis* from Madagascar were assumed to have a direct developmental mode, *i.e.*, the complete embryonic and larval development within the egg, but recently free-swimming, exotropic tadpoles of a few species have been found. Herein we provide detailed morphological descriptions of the tadpoles of five more species of this genus, indicating a developmental mode other than direct development in further species of *Gephyromantis*. Tadpoles of *Gephyromantis granulatus*, *G. sculpturatus*, *G. tschenki* and *G. ventrimaculatus* were found free-swimming in streams, and tadpoles of *G.* sp. aff. *blanci* were raised after hatching from clutches found in the leaf litter. All tadpoles were identified by DNA barcoding. The oral disks of all five species are characterized by the lack of many typical morphological traits of exotrophic tadpoles (such as oral papillae and keratodonts), indicating that these tadpoles are either non-feeding (endotrophic) or only facultatively feeding tadpoles. We classify these tadpoles as nidicolous based on the observation that the larvae of *G.* sp. aff. *blanci* stayed after hatching in the jelly nest until metamorphosis. It remains an open question whether all species have strictly nidicolous tadpoles and the larvae of the four species found in the streams were just accidentally washed into these streams, or they are nidicolous at first but in some species need to live in free water at later stages.

Key words: Amphibia, *Gephyromantis*, oral disk, tadpole morphology, exotrophic, endotrophic, direct development, nidicolous, generalized, carnivorous tadpoles, ecomorphological guilds.

Introduction

Tadpole, the larval stages of anuran amphibians, is becoming increasingly the subject of biological research. There is a need for reliable identification of these larvae particularly in tropical environments where amphibian diversity is highest. Tadpoles are present in aquatic habitats for longer periods than breeding adults and are often more easily collected. Understanding the diversity for tadpole morphology is a prerequisite of successful identification. Appreciating how those morphologies are distributed across taxa and which tadpoles have been described in each group is an important basis for further research (Altig & McDiarmid 1999b).

In the classification of developmental modes of amphibians, endotrophy is defined as the usage of a maternal source of energy during the larval development and exotrophy is defined as the usage of energy from food for the development. Altig & Johnston (1989) defined a high number of developmental guilds for exotrophs, and six for endotrophs. Examples of the exotrophic developmental modes are typical lentic-bentic, filter-feeding nectonic, or carnivorous

Figure 1. Coloration in life of tadpoles of four species of *Gephyromantis* in dorsal, lateral and ventral views: **a** – *G. sculpturatus* (ZSM 16/2008 – ZCMV 4833); **b** – *G. tschenki* (ZSM 142/2007 – ZCMV 4335); **c** – *G. ventrimaculatus* (ZSM 852/2007 – ZCMV 4927); **d** – *G. azzurae* (ZSM 1922/2007 – T 2007-511). The scale bars represent 1 mm.

tadpoles that feed on macroinvertebrates and conspecific and heterospecific tadpoles. The six endotrophic developmental modes proposed by Altig & Johnston (1989) are *(1)* viviparous (after exhaustion of vitellogenic yolk, the fetus in the oviduct feeds on oviducal materials to complete a modified development before birth as a froglet), *(2)* ovoviviparous (the embryo completes a modified development in the oviduct via only oogenic energy sources and is born as a froglet), *(3)* paraviviparous (embryo completes a modified development via oogenic energy source in a site other than the reproductive tract of the female and is "born" as a froglet), *(4)* exoviviparous (embryo develops via oogenic energy sources in a terrestrial egg before the hatchling moves to a site usually in or on the male parent's body and a froglet eventually is born from that site), *(5)* direct developer (embryo completes highly modified development via oogenic energy sources in an deposited egg that is not intimately associated with parent's body and hatches as a froglet), and *(6)* nidicolous (terrestrial oviposition, and embryo develops from oogenic energy sources to produce various sorts of free-living, non feeding larvae). Exotrophic development, in anurans, is supposed to be the ancestral reproductive mode, but endotrophic development is surprisingly common with two endotrophic lineages in the leptodactylids sensu lato, one endotrophic guild each in hylids, rhacophorids, and megophryids, and endotrophic taxa in six of ten subfamilies of microhylids (Thibaudeau & Altig 1999).

Despite the existence of these quite precise definitions, in practice hypotheses of endotrophic development in many species are based solely on the observation of clutches of only few, large, and usually nonpigmented ovarian eggs. Eggs of endotrophic species usually are larger than those of similar size frogs with exotrophic tadpoles and are deposited in sites with sufficient moisture (Thibaudeau & Altig 1999). Based on the known relationship between egg size and pigmentation, also among species with exotrophic larvae breeding in different environments, this criterion should, however, be employed cautiously.

In the highly diverse frog fauna of Madagascar, with probably over 400 species including as yet undescribed ones (Vieites et al. 2009), two clades of frogs are known to show endotrophic development: *(1)* The subfamily Cophylinae, a Madagascar-endemic clade of the family Microhylidae; Its species have nidicolous development, with non-feeding tadpoles developing in water-filled tree holes, bamboo nodes or leaf axils, or in terrestrial jelly or foam nests (Blommers-Schlösser 1975). *(2)* Endotrophic development has been described for the genus *Gephyromantis*, a genus in the Madagascar-endemic family Mantellidae (Blommers-Schlösser 1979; Glaw & Vences 1994). Historically, and based mainly on observations of Blommers-Schlösser (1979), on eggs putatively belonging to *Gephyromantis asper,* and of Glaw & Vences (1994) on a clutch of *G. eiselti,* direct development has been stated to occur in this clade. A general prevalence of such a direct mode of development in the clade that is now considered to be the genus *Gephyromantis* (see Glaw & Vences 2006) has since generally been assumed. This is in agreement with the observation of

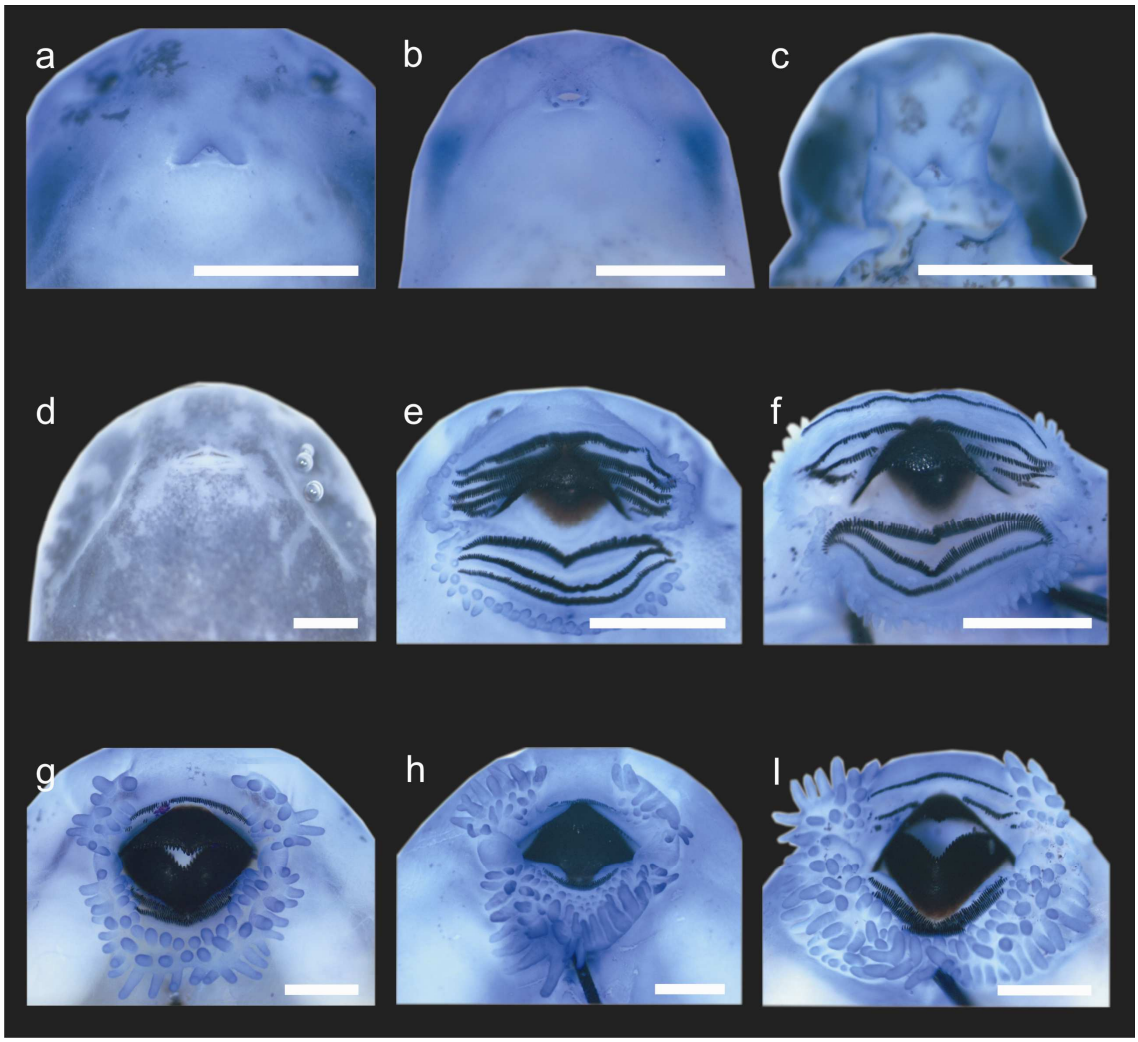

Figure 2. Photographs of the oral disk of the preserved voucher specimens of tadpoles described in this paper (stained with methylene blue): **a** – *Gephyromantis granulatus* (ZSM 298/2008 – Tad 2004-75); **b** – *G. sculpturatus* (ZSM 16/2008 – ZCMV 4833); **c** – *G. tschenki* (ZSM 142/2007 – ZCMV 4335); **d** – *G. ventrimaculatus* (ZSM 852/2007 – ZCMV 4927); **e** – *G. ambohitra* (ZSM 756/2004 – FGMV 2003-1946); **f** – *G. asper* (ZSM 1912/2007 – ZCMV 3401); **g** – *G. azzurae* (ZSM 1922/2007 – T 2007-511); **h** – *G. corvus* ZSM 0674/2008 – T 001); **i** – *G. pseudoasper* (ZSM 707/2004 – FGMV 2003-1919). The scale bars represent 1 mm.

Thibaudeau & Altig (1999) that if endotrophy occurs in a presently recognized genus, usually all species involved are in the same guild which is a monophyletic group according to molecular data (*e.g.*, Glaw & Vences 2006; Vieites et al. 2009).

However, uniformity of developmental mode in *Gephyromantis* has been challenged already by the observation of Glaw & Vences (1994) of metamorphosing tadpoles probably to be assigned to *G. granulatus*. In addition, exotrophic tadpoles have become known from various species that phylogenetically are firmly embedded in the genus: *G. ambohitra* and *G. pseudoasper* have generalized and carnivorous tadpoles, respectively (Randrianiaina et al. 2007).

During a large-scale survey of tadpoles in Madagascar, based on reliable species identifications by DNA barcoding, we have been able to collect additional data on the tadpoles of *Gephyromantis*. We observed five additional exotrophic tadpoles: *G. asper*, *G.* sp. aff. *asper*, *G.* sp. aff. *ambohitra*, *G. corvus* and *G. azzurae*. The first three are generalized and the last two are carnivorous. These larvae will be described in more detail in forthcoming papers. Here we focus on those tadpoles with strongly reduced oral disks and mouth openings that we hypothesize are endotrophic, and that we identified genetically as belonging to *G. granulatus*, *G. sculpturatus*, *G. tschenki*, *G. ventrimaculatus* and *G.* sp. aff. *blanci*. We describe the external morphology of these tadpoles and present data on the embryonic and larval development of *G.* sp. aff. *blanci* from a rearing experiment. The intention is to understand their developmental mode. We argue that none of these tadpoles qualifies as direct developer and that probably only one kind of endotrophic developmental mode – nidicolous tadpoles – is present in Malagasy anurans.

Materials and methods

Tadpoles were collected using different kinds of nets having mesh sizes from 2 to 5 mm, depending on the size of stream, the strength of the current and the type of substrate. Specimens were euthanised by immersion in chlorobutanol solution, and immediately sorted into homogeneous series based on morphological characters. From each series one specimen was selected and a tissue sample from its tail musculature or fin taken and preserved in 99% ethanol. This specimen is here named "DNA voucher". All detailed morphological tadpole characterizations and drawings are based on this DNA voucher, whereas variation is described based on further specimens of the series, if such specimens exist. However, since the tadpoles described in this paper were mostly not common In many cases, the series consist of single individuals only. After tissue collection, all specimens were preserved in 5% formalin or 70% ethanol. Specimens were deposited in the Zoologische Staatssammlung München, Germany (ZSM). Tadpoles were identified using a DNA barcoding approach based on a fragment of the

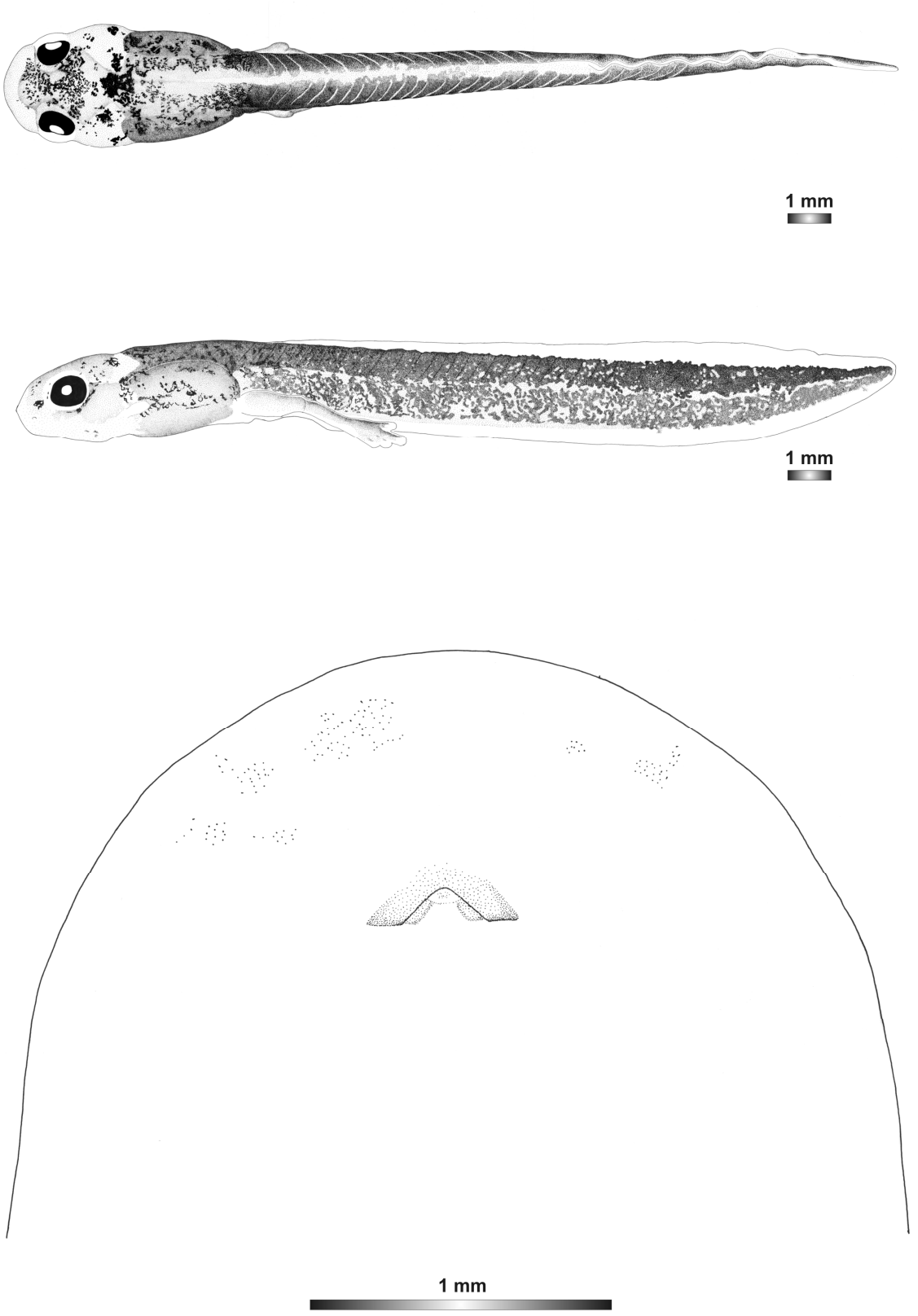

Figure 3. Drawings of the preserved DNA voucher tadpole of *Gephyromantis granulatus* (ZSM 298/2008 – Tad 2004/75): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

mitochondrial 16S rRNA gene, which is known to be sufficiently variable among species of Malagasy frogs (Thomas et al. 2005). The ca. 550 bp fragment was amplified using primers 16Sar-L and 16Sbr-H from Palumbi et al. (1991) applying standard protocols (Vences et al. 2005), resolved on automated sequencers, and compared to a near-complete database of sequences of adult Malagasy frog species. Identification was considered to be unequivocal when the tadpole sequence was 99–100% identical to an adult specimen from the same geographical region, and clearly less similar to all sequences from other species. DNA sequences were deposited in Genbank (accession numbers GU975156, GU975158, and HQ188939-HQ188941).

Developmental stages were assigned following the scheme proposed by Del Pino & Escobar (1981) for endotrophic frogs. However, because of substantial differences in the development of different morphological structures in different endotrophic species, we also attempted to assign stages according to the scheme of Gosner (1960) that is widely used for exotrophic tadpoles. Del Pino & Escobar (1981) and Gosner (1960) were used for *Gephyromantis* sp. aff. *blanci*, and only Gosner (1960) was used for *G. granulatus*, *G. sculpturatus*, *G. tschenki*, *G. ventrimaculatus* because there is no equivalence of the developmental stage according to Gosner (1960) upper than 37 in Del Pino & Escobar (1981) system. Description, morphological measurements, and drawings were done on pictures taken with a stereomicroscope Zeiss Discovery V12 connected to a computer, following landmarks, terminology and definitions of Altig & McDiarmid (1999a) and Randrianiaina et *al.* (submitted), except the that we predominantly use the term keratodonts instead of labial teeth. The formula of keratodonts (= labial tooth row formula, LTRF) is given according to Altig & McDiarmid (1999). Drawings and photographs of the preserved tadpoles are shown in Figures 2-7. Comparing measurements, we consider them as almost equal if ratios of the measured values are 95–96% or 104–105%, and equal if they are in the range 97-103%.

The following abbreviations are used: A_1 (first upper keratodont row), A_2 (second upper keratodont row), A_{2gap} (medial gap in row A_2), A_3 (third upper keratodont row), A_4 (fourth upper keratodont row), A_5 (fifth upper keratodont row), $A_{1\text{-}5\ den}$ (density of the keratodonts in row $A_{1\text{-}5}$), $A_{1\text{-}5\ len}$ (length of the row $A_{1\text{-}5}$), $A_{1\text{-}5\ num}$ (number of keratodonts in row $A_{1\text{-}5}$), BH (maximal body height), BL (body length), BW (maximal body width), DF (dorsal fin height at midtail), DG (size of the dorsal gap of marginal papillae), DMTH (distance of maximal tail height from the tail-body junction), ED (eye diameter), EH (eyes height - measured from the lower curve of the belly), HAB (height of the point where the axis of the tail myotomes contacts the body - measured from the lower curve of the belly), IND (inter-narial distance - measured from the center), IOD (inter-orbital distance - measured from the center), JW (maximal jaw sheath width), MC (medial convexity of the upper sheath), MCL (length of the medial convexity of the upper sheath), MP (marginal papillae), MTH (maximal tail height), ND (naris diameter), NH (naris height - measured

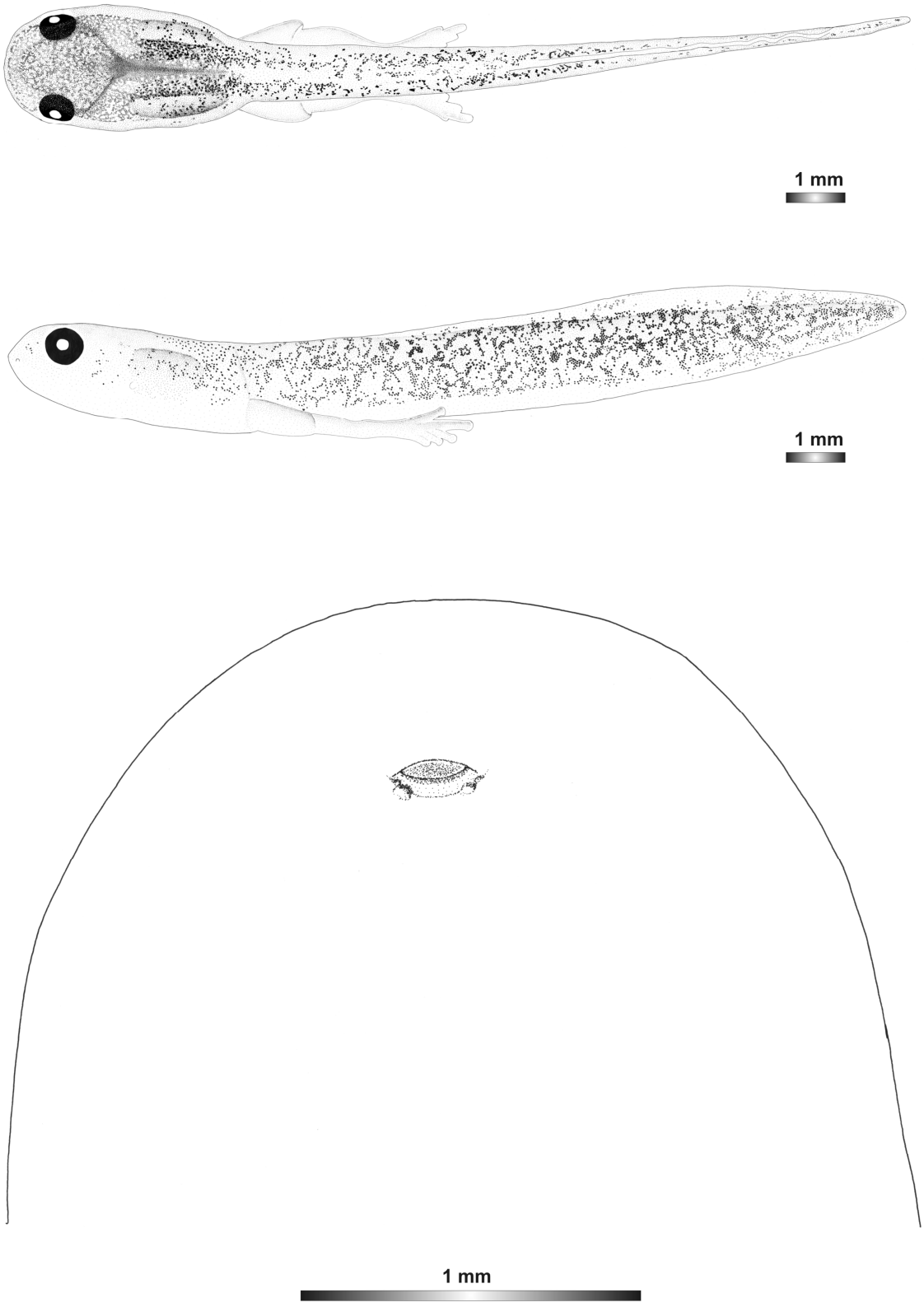

Figure 4. Drawings of the preserved DNA voucher tadpole of *Gephyromantis sculpturatus* (ZSM 16/2008 – ZCMV 4833): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

from the lower curve of the belly), NP (naris-pupil distance), OD (oral disk), ODW (maximum oral disk width), P_1 (first lower keratodont row), P_2 (second lower keratodont row), P_3 (third lower keratodont row), $P_{1\text{-}3\ den}$ (density of the keratodonts in row $P_{1\text{-}3}$), $P_{1\text{-}3\ len}$ (length of the row $P_{1\text{-}3}$), $P_{1\text{-}3\ num}$ (number of keratodonts in row $P_{1\text{-}3}$), RN (rostro-narial distance), SBH (distance between snout and the point of maximal body height), SBW (distance between snout and the point of maximal body width), SE (snout-eye distance), SH (spiracle height - measured from the lower curve of the belly), SL (spiracle length), SMP (submarginal papillae), SS (snout-spiracle distance), SV (spiracle-vent distance), TAL (tail length), TH (tail height at the beginning of the tail), THM (tail height at mid-tail), Thorn-pap (thorn-shaped papillae), TL (total length), TMH (tail muscle height at the beginning of the tail), TMHM (tail muscle height at mid-tail), TMW (tail muscle width at the beginning of the tail), LR (number of the lower rows of keratodonts), UR (number of the upper rows of keratodonts), VF (ventral fin height at midtail), VG (size of the ventral gap of marginal papillae), VL (vent tube length).

Results

This part include just a brief account of mainly one characteristic species Detailed descriptions and assessment of variation are found in the descriptions in the appendix.

Gephyromantis granulatus (Boettger 1881)

The following description refers to one tadpole (Figures 2, and 3) in developmental stage Gosner 40 Field number Tad 2004–75 - ZSM 298/2008, BL 5.8 mm, TL 20.7 mm) collected by R.D. Randrianiaina, M. Puente and F. Glaw on 19-23 February 2004 in Montagne d'Ambre National Park in a brook crossing the track "Voie des milles arbres" (coordinates at stream not taken, but not far from 12°31.667'S, 49°10.667'E, 1050 m a.s l.). The 16S rDNA sequence of this specimen was 100% identical to the reference sequence of a *G. granulatus* adult specimen (accession AJ315926) in Genbank. Nineteen non vouchen specimens of the same series present the typical morphology of the voucher specimen.

The larval stages of this genus are filiform tadpoles characterized by having just a triangular mouth opening instead of the typical oral disk structure, small round nares, positioned low laterally and oriented ventrally, and a very long tail (TAL 305% of BL). In preservative they are predominantly pale-brownish. Light pale brown melanophoric pigment covers the dorsum. Dark brown patches scattered irregularly on the skin and condensed to form dark patches especially above the neuro cranium and the whole dorsum. Ventrally, oral disk, gular and

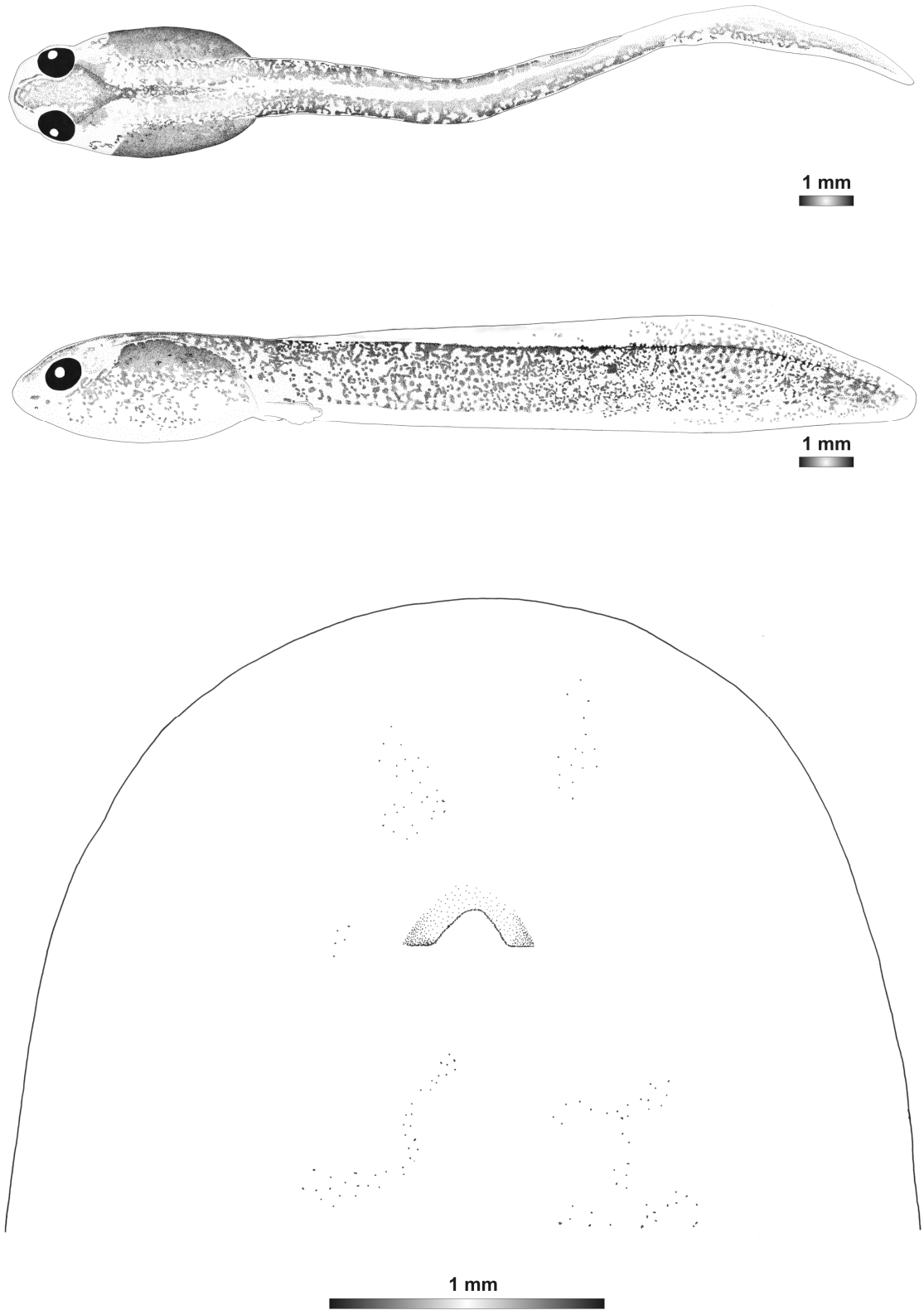

Figure 5. Drawings of the preserved DNA voucher tadpole of *Gephyromantis tschenki* (ZSM 142/2007 – ZCMV 4335): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

branchial regions beige with a few blotches; venter covered by light brown condensed reticulations, no intestinal coils visible. Tail musculature overlaid by dense light brown reticulations leaving the lateral line conspicuous all along the tail. Fins are pale and unpigmented.

Gephyromantis sculpturatus (Ahl 1929)

The following description refers to one tadpole (Figures 1, 2, and 3) in developmental stage Gosner 39 (Field number ZCMV 4833 - ZSM 16/2008, BL 6 mm, TL 18 mm) collected by R.D. Randrianiaina, A. Strauß, E. Reeve, J. Glos, S..Ndriantsoa, and T. Rasolonjatovo H. on 11 February 2007 in Ranomafana National Park at Piste X 175 site (21°15.846' S 47°25.161' E, 966 m a.s.l.). The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of a *G. sculpturatus* adult specimen (accession AY848432) from the same locality.

The larval stages of this genus have the same morphotype with those of *Gephyromantis granulatus* except that they have an elliptical mouth opening with two papillae and their pigmentation is sparser. In life, they are typically yellowish and covered by brown variegated melanophoric pigments and some silver irridophoric spots or patches.

Gephyromantis tschenki (Glaw & Vences2001)

The following description refers to one tadpole (Figures 1, 2, and 3) in developmental stage Gosner 35, Del Pino and Escobar 23-25 (Field number ZCMV 4335 - ZSM 142/2007, BL 4.6 mm, TL 16.7 mm) collected by R.D. Randrianiaina, A. Strauß, E. Reeve, J. Glos, S..Ndriantsoa, and T. Rasolonjatovo H. on 25 February 2007 in Ranomafana National Park at Bibiango site (21°15.442' S 47°25.096' E, 962 m a.s.l.). The 16S rDNA sequence of this specimen was 98.5% identical to a reference sequence of *G. tschenki* adult specimen (accession AY848374) from the same locality.

The larval stages of this genus have the identical morphotype with those of *Gephyromantis granulatus* by the triangular mouth opening. The only difference is just encountered in the sparse pigmentation that *Gephyromantis tschenki* larvae have.

Gephyromantis ventrimaculatus (Angel 1935)

The following description refers to one tadpole (Figures 1, 2, and 3) in developmental stage Gosner 39 (Field number ZCMV 4927 - ZSM 852/2007, BL 6.4 mm, TL 20.4 mm) collected by R.D. Randrianiaina, A. Strauß, E. Reeve, J. Glos, S..Ndriantsoa, and T. Rasolonjatovo H. on 02 March 2007 in Ranomafana National Park at Sahateza site (21°15.453' S

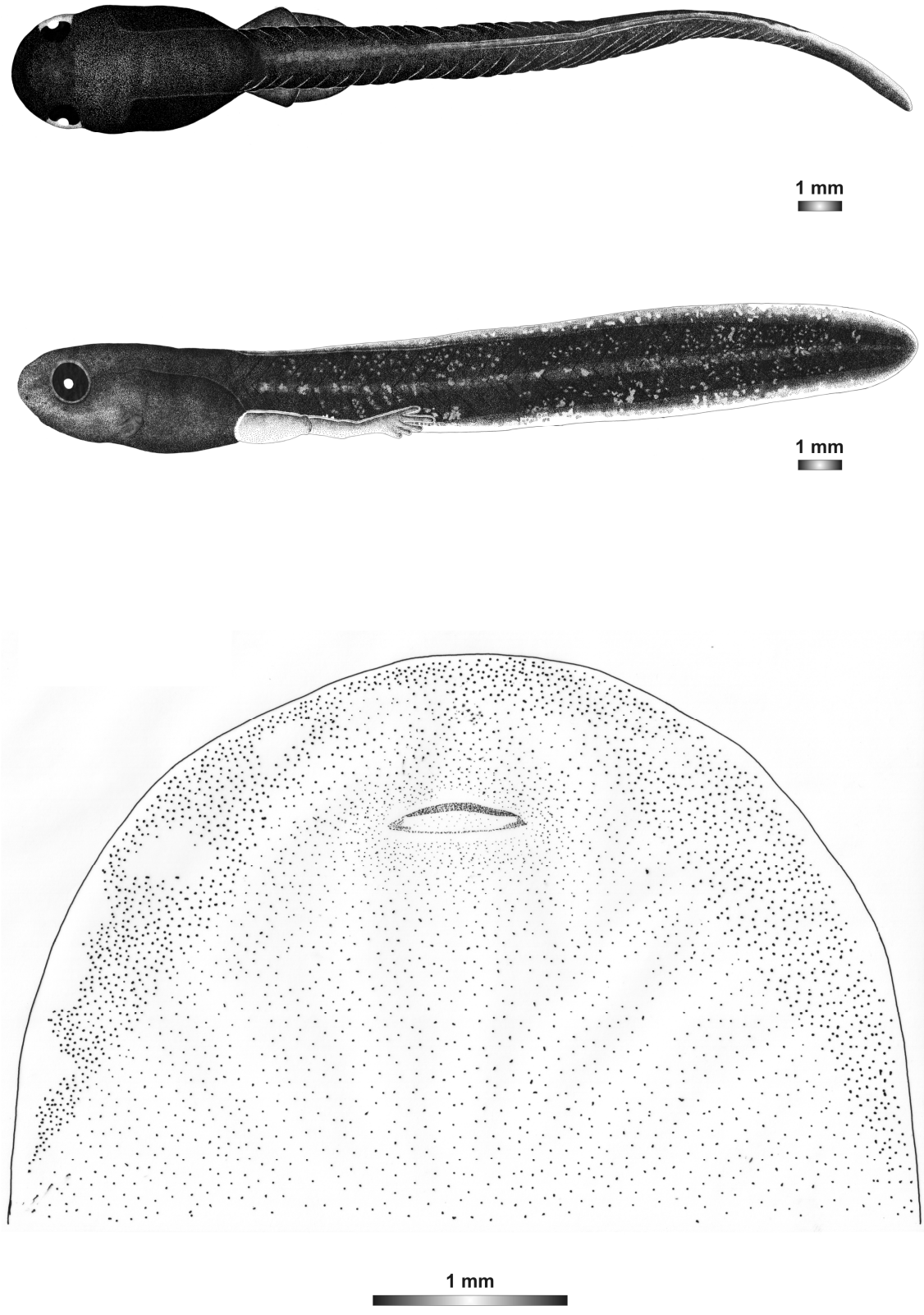

Figure 6. Drawings of the preserved DNA voucher tadpole of *Gephyromantis ventrimaculatus* (ZSM 852/2007 – ZCMV 4927): **a** – Dorsal view; **b** – Lateral view; **c** – Oral disk.

47°21.609' E, 1164 m a.s.l.). The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of *G. ventrimaculatus* adult specimen (accession FJ559200) from Ranomafana (Ranomafanakely).

The larval stages of this genus have the identical morphotype with those of *Gephyromantis granulatus*, *Gephyromantis sculpturatus*, and *Gephyromantis tschenki*, but they are easily recognized by their typical dark coloration. The elliptical mouth opening is identical to those of *Gephyromantis sculpturatus*.

Gephyromantis sp. aff. *blanci*

These data refer to a population of small, terrestrial and diurnal frogs from Ranomafana National Park considered as *G. blanci* by Vieites et al. (2009). However, our own unpublished molecular and bioacoustic data indicate that in fact this population represents an undescribed candidate species that we here refer to as *G.* sp. aff. *blanci*. A clutch of four eggs was collected by K.C. Wollenberg on 5th March 2007 in Ranomafana National Park at a site locally known as Ranomafanakely (21° 14.921' S, 47° 22.307' E, 1134 m a.s.l.). Weather conditions were moist with constant rain at the time when the clutch was found. The site contained a forested slope, overgrown with lianae and moss. On the bottom of the slope, a ca. 10cm thick layer of leaf litter covered the forest floor. Many males of *G. enki* were calling from here. At the more elevated positions of the slope, dead wood overgrown with moss was under the leaf litter. It was forming a thick, porous layer with many cavities of up to 1m depth. The clutch was found on such a cavity overgrown with moss, but was partially exposed to daylight and attached to the surface of a dead leaf. Rain water was dripping on the clutch from the moss layer above it. The clutch was found while searching for a male specimen of *G.* sp. aff. *blanci* that was calling approximately 30cm from the clutch from an elevated position. Other specimens of *G.* sp. aff. *blanci* were heard calling from other sites further up the slope. We suspect that the eggs might have guarded by the male, as this behaviour has been observed in other species of the *G. boulengeri* group (own observations). The clutch was taken to the lab, and one egg was immediately removed and preserved with field number ZCMV 5253 in 90% ethanol for species identification by DNA-barcoding. The remaining three eggs remained on the leaf and were kept in a terrarium with leaf litter, and watered regularly. Their development was followed for 24 days until the last metamorph left the clutch. A single egg had a diameter of about 3 mm, the yolk being pale yellow in a transparent jelly.

Development of embryos and larvae (Fig. 7): When observation started on day 1 after collection (6 March), pale white/yellow embryos were visible. Due to the beginning of tail

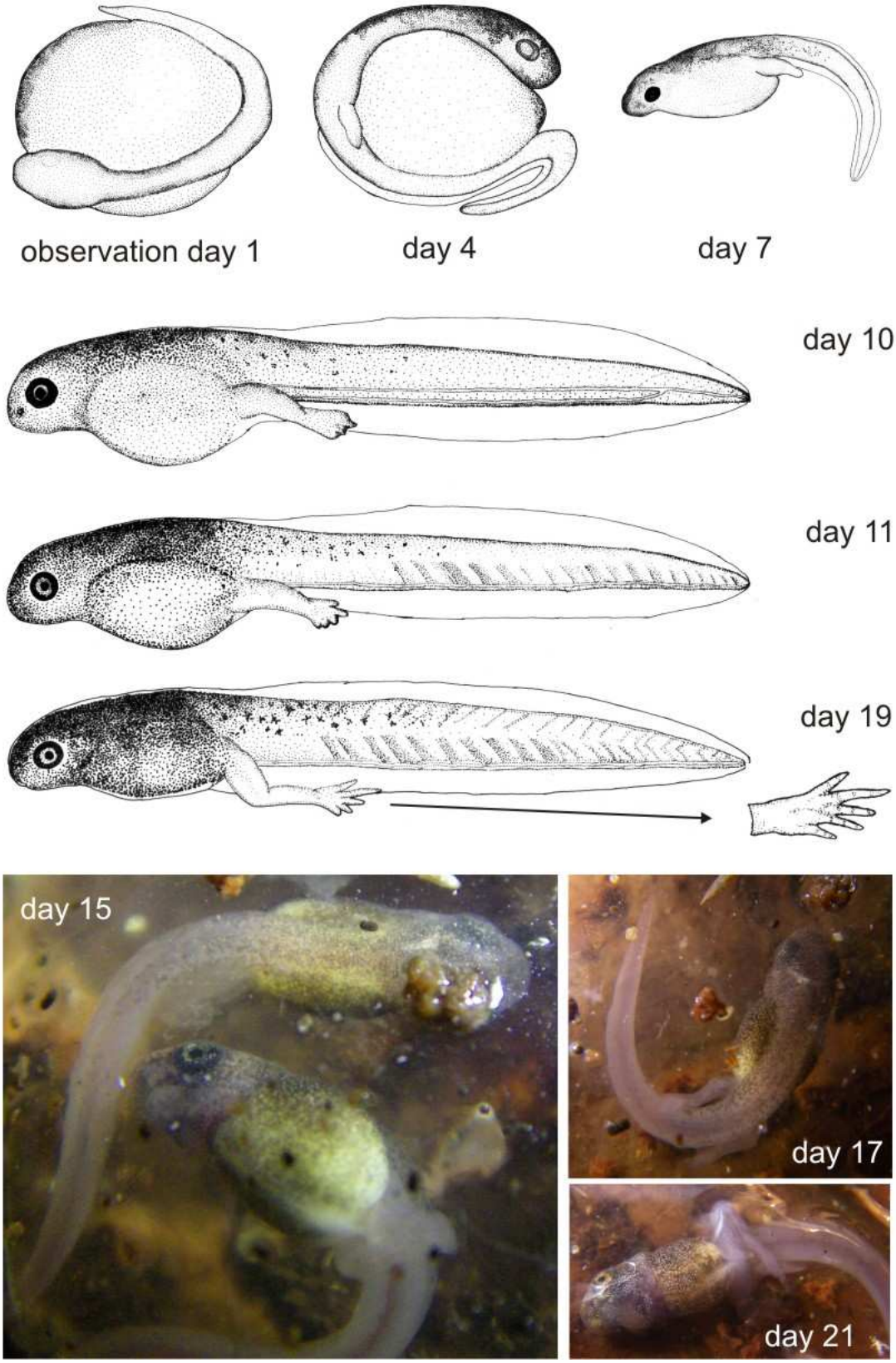

Figure 7. Larval development of *Gephyromantis* sp. aff. *blanci* from Ranomafana. Drawings were made on the basis of photographs of living specimens and are not to scale. Time is given as days after collection of the clutch; the actual time since egg deposition is unknown. Note in the photographs in ventral view that the larvae in comparatively early stages appear to have a developed mouth with jaws (no tadpole-like oral disk).

development, the embryo fitted stages 17/18 according to Gosner (1960) or stage 13 according to Del Pino and Escobar (1981).

On day 3 the embryos showed very weak pigmentation, and the outline of the eye was visible.

On day 4 TAL reached about 120% of BL, ED about 8% of BL, and the tail had transparent fins. The beating heart was visible. The cornea was transparent. Also, there was clear tail elongation allowing first movements (hatchling stage according to Gosner 1960; staging after DelPino and Escobar 1981 not applicable). Arteries across the yolk were formed.

On day 7 TAL was about 170% of BL, ED about 15% of BL. Toe differentiation and development, indentation 4-5. Vitellus volume diminished, tail mainly free. Cornea visible. Body dorsally pigmented.

On day 10 TAL was 193% of BL, ED 17% of BL. Indentation 2-3, vitellus reduced by about 1/3 compared to day 7. Blood vessel in posterior part of caudal musculature visible. Nares visible. Body more pigmented. Jelly of two tadpoles united.

On day 11 TAL about 180% of BL, ED 16% of BL. Transverse muscular structures visible. Pigmentation increasing laterally to ventrally. Indentation 1-2.

On day 13 and 14 (18 and 19 March), TAL 177% of BL. ED 9% of BL and TAL 211% of BL, ED 15% of BL. Toe 3-5 separated.

On day 16 TAL 200% of BL, ED 12% of BL. All toes separated, the outline of the mouth is visible.

On day 17, TAL 177% of BL, ED 15% of BL . Subarticular patches.

On day 19 and 20 TAL 210% of BL, ED 16% of BL and TAL 180% of BL, ED 15% BL, foot tubercles visible, vent tube present.

On day 24 the last hatchling left the jelly with four well developed legs and a tail of about 126% of BL.

The following description refers to one metamorphosed froglet in Gosner stage 44 (ZSM 649/2008, BL 5.3 mm TL 9 mm) from the batch described above. In dorsal view, body elliptical, maximal body width attained between the proximal 3/5 and 4/5 of the body (SBW 64% of BL), broadly rounded snout. In lateral view, body depressed (BW 112% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 72% of BL), rounded snout. Large eye (ED 17% of BL), visible from ventral view, positioned moderately high (EH 52% of BH) laterally and directed laterally, situated between the proximal 2/10 and 3/10 of the body (SE 22 % of BL), wide distance between eyes (IOD 87% of BW). Small rounded nares (ND 1.9% of BL), countersunk, positioned low (NH 34% of BH) laterally and oriented ventrally, situated nearer to snout than to eye (RN 70% of NP), moderately wide distance between nares (IND 58% of IOD), no dark spot on the back of the nares, ornamentation absent. No spiracle or vent tube visible. Tail is largely resorbed, therefore very short tail (TAL 126% of BL).

Moderately large oral disk (ODW 42% of BW), not connected to snout, positioned and directed ventrally. Oral disk already being transformed into a frog mouth structure. Yellow structure, probably the tongue, visible inside the mouth. All the typical structures of the oral disk of a tadpole absent.

Coloration in preservative: General coloration yellowish. Body dorsum, laterally and abdominal surface covered by light brown reticulations. Gular and branchial regions brown, intestinal coils not visible, tail musculature covered by some blotches.

Discussion

1. Morphological diversity of *Gephyromantis* larvae

Since Blommers-Schlösser (*e.g.*, 1975, 1979) first integrated life history observations in the general systematic assessment of Malagasy anurans and, thereby, for the first time elaborated a classificatory system reflecting their biological (evolutionary) relationships. Species that today are included in the genus *Gephyromantis* had assumed to have direct development. New observations (Glaw & Vences 1994; Vences & Glaw 2001) then challenged this assumption and provided evidence for endotrophic as well as exotrophic development in this lineage. However, all these early observations were preliminary and not based on reliable identifications of the larvae or embryos examined. This changed with the work of Randrianiaina et al. (2007) who not only reported reliably (based on molecular species identification) exotrophy in tadpoles of *G. ambohitra* and *G. pseudoasper* but also provided detailed morphological descriptions of these.
Subsequently we have found further exotrophic tadpoles in *G. asper*, G. sp. aff. *asper*, G. sp. aff. *ambohitra* "Marojejy", *G. corvus*, and *G. azzurae* (own observations; unpublished data). Some of these larvae are generalized tadpoles but the others appear to be carnivorous because of the presence of hypertrophied jaw sheaths.

Herein we provide the first detailed morphological descriptions of putatively endotrophic *Gephyromantis* tadpoles of five species that belong to three different subgenera within the genus: *Duboimantis* (*G. granulatus*, *G. sculpturatus*, *G. tschenki*), *Laurentomantis* (*G. ventrimaculatus*), and the nominal subgenus *Gephyromantis* (G. sp. aff. *blanci*). The discovery and study of these larvae has yielded two main surprising insights: *(1)* None of these larvae had direct development, although this had been assumed at least for the subgenera *Gephyromantis* and *Laurentomantis* (*e.g.*, Glaw & Vences 1994); and *(2)* the larvae of *Duboimantis* and *Laurentomantis* were found free-swimming in streams rather than in terrestrial nests.

The diversity of developmental modes within *Gephyromantis* is exceptional. Of the five existing subgenera (*Gephyromantis*, *Vatomantis*, *Laurentomantis*, *Phylacomantis* and *Duboimantis*) (Glaw & Vences 2006), the only subgenus for which no data on the larval development are available is *Vatomantis*. For one representative of this subgenus, *G. webbi*, it is known, however, that clutches of a few large eggs are deposited on rocks overhanging small streams (Andreone 1993; Glaw & Vences, 1994). We therefore suspect that in this species too, endotrophic tadpoles will hatch from these eggs and complete their development free-swimming in the stream; similar to what we here report for *Laurentomantis* and *Duboimantis*. Three different ecomorphological guilds of tadpoles can thus be distinguished among the subgenera of *Gephyromantis*: the first is the generalized tadpoles of *G. ambohitra* (Randrianiaina et al. 2007), *G.* sp aff. *ambohitra*, and *G. asper* (pers. obs., unpublished data), the second is the carnivorous tadpoles of *G. pseudoasper* (Randrianiaina et al. 2007), *G. corvus*, and *G. azzurae* (pers. obs., unpublished data), and the third are the non-feeding tadpoles described in this study.

The first guild, "generalized", is characterized by a short tail, a moderately developed caudal musculature, a small to moderately large oral disk (ODW 38% of BW), moderately large and fully keratinized upper jaw sheaths (JW 51 to 53% of ODW), an upper jaw sheath having a very short widely rounded medial convexity (MCL 2 to 5% of JW) and rounded serration, a lower jaw sheath half keratinized and partially hidden by the upper ones, small (MP 0.12 mm, SMP 0.09 to 0.11 mm) and few papillae (MP 63 to 96, SMP 4 to 10) with rounded tips, a wide dorsal gap of papillae (DG 69 to 75% of ODW), an absence of a ventral gap of papillae, a LTRF of 5(2-5)/3(1) (after Altig & McDiarmid 1999), small keratodonts (0.12 mm), normal lower tooth rows (not scattered as in a few other mantellids, *e.g.*, *Mantidactylus femoralis*), and a very narrow A_2gap (6 to 8% of A_2). Tadpoles agreeing with this morphology have been described for *G. ambohitra* (Randrianiaina et al. 2007), and also for *G. asper*, *G.* sp. aff. *asper*, and *G.* sp. aff. *ambohitra* (Fig. 2; unpublished data). These species have been provisionally classified in the subgenus *Duboimantis* (see Glaw and Vences 2006) but they together form a monophyletic group within the genus *Gephyromantis* whose affinities have not yet been solved (Vences & Glaw 2001; Vieites et al. 2009). Given their developmental mode different from other *Duboimantis*, these species should be placed in a separate subgenus.

The second guild of carnivorous tadpoles is characterized by a short tail, a moderately developed caudal musculature, a small to moderately large oral disk (ODW 34 to 42% of BW), moderately large and fully keratinized upper jaw sheaths (JW 46 to 57% of ODW), an upper jaw sheath having a very short narrowly pointed medial convexity (MCL 3 to 4% of JW) and hypertrophied serration, a V-shaped fully keratinized lower jaw sheath and partially hidden by the upper ones, large elongated (MP 0.42 to 0.57 mm, SMP 0.15 to 0.38 mm) and few papillae (MP 39 to 58, SMP 47 to 72) with rounded tips, a small to moderately wide dorsal gap of papillae (DG

30 to 48% of ODW), an absence of a ventral gap of papillae, a LTRF of 2(2)/1 and 3(2-3)/3(1) (after Altig and McDiarmid 1999), small keratodonts (0.08 to 0.13 mm), normal lower tooth rows, and a very narrow to very wide A_2gap (27 to 92% of A_2). All nominal species in the subgenus *Phylacomantis* have tadpoles agreeing with this morphology, and it is likely that similar tadpole morphology also is present in the so far undescribed candidate species assigned to this subgenus (see Vieites et al. 2009). These larval characters therefore seem to constitute synapomorphies for the clade including: *G. pseudoasper* (Randrianiaina et al. 2007), and *G. azzurrae and G. corvus* (Figure 2; unpublished data).

The third guild comprises the non feeding tadpoles described in this study. These larvae are characterized by a small mouth opening (8 to 19% of BW) lacking the usual components of tadpole oral disks, except for *G. sculpturatus* which has four small papillae, a small body size (maximal BL 6.4, BW 3.6, BH 3.1 mm), a very long tail (TAL > 300% of BL), very low fins (DF 18–24% of TMHM, VF 20–23% of TMHM), laterally situated and directed eyes, laterally positioned and ventrally oriented nares. These putatively endotrophic *Gephyromantis* tadpoles are easily distinguished from other mantellid tadpoles by their small body size, small mouth, and their very long tail and very low fins. Their eyes are situated laterally and directed laterally. Having laterally positioned and ventrally oriented nares is unique to these tadpoles. The function of their small mouth opening is not clear, whether it is used only gill irrigation, for air gulping, or to some degree or at some stage also for feeding. Tadpoles fitting this morphology occur in *G. granulatus*, *G. sculpturatus*, *G. tschenki*, *G. ventrimaculatus*, and *G.* sp. aff. *blanci* (*Duboimantis*, *Gephyromantis*, and *Laurentomantis*). Of these, we assume that species in the nominal subgenus *Gephyromantis*, which in their adult phase are small, diurnal frogs always calling independent from water bodies, are obligatory nidicolous, *i.e.*, tadpoles complete their development within terrestrial jelly nests, whereas species in the other two subgenera have larvae that are partially or optionally nidicolous, *i.e.*, they can complete their development free-swimming in streams.

2. Nidicolous tadpoles in *Gephyromantis*

Our assumption of endotrophic development in the species studied herein is based on the combination of comparatively small size, lack of visible intestinal coils and rudimentary mouthparts. However, in all of them a mouth opening was recognizable and we can thus not fully exclude that these larvae ingest some kind of food at some stage of larval development although in *G.* sp. aff. *blanci* we did not observe food ingestion during the whole development. Thibaudeau & Altig (1999) mentioned that among endotrophic tadpoles, morphological diversity is highest

among the nidicolous group where various developmental patterns provide a wide range of morphotypes.

Except for the larvae of *G.* sp. aff. *blanci* that were reared from a clutch found close to an area where adult males of the species were calling, we captured all tadpoles in flowing streams and not in tree holes or terrestrial nests as is typical for cophyline microhylid tadpoles in Madagascar. We assume that these larvae stay some days in the stream and complete their development there, because we found series of tadpoles in stages ranging from newly hatched (without limbs) to close to metamorphosis (with four limbs but still with long tail). Since no inequivocally identified egg clutches of species in the subgenera *Duboimantis* and *Laurentomantis* have been so far found It is at present not possible to ascertain whether it is an integral part of their reproductive strategy that larvae complete their development in water, or if the tadpoles encountered by us had just accidentally been washed into streams by heavy rainfalls from their nests. *Gephyromantis* are semiarboreal frogs that can be found on the forest floor but often climb onto the low vegetation, and many species are regularly found in the vicinity of streams. It is obvious that the adults lay their eggs neither on leaves hanging above water body, nor in any substrate close to or in the water nor directly in the water (Glaw & Vences, 1994, 2007) like other, related semiarboreal or arboreal frogs in the genera *Blommersia*, *Guibemantis*, and *Spinomantis*. Especially clutches exposed on leaves would almost certainly not have passed unperceived during our intensive herpetological surveys in Ranomafana National Park and elsewhere in Madagascar.

Compared to most other tadpoles (Strauß et al. 2010), the endotrophic *Gephyromantis* tadpoles were very rare in the streams of Ranomafana National Park. Of the 7,020 respectively 8,399 tadpoles collected in wet season 2007 and 2008, and the 1,201 tadpoles collected in the dry season 2008, we found only six individuals of *G. ventrimaculatus*, two of *G. sculpturatus*, and one of *G. tschenki* tadpoles, although at least two of these species (*G. sculpturatus* and *G. tschenki*) are common and easily observed frogs in the Park. This corresponds to only 0.0005% of all tadpoles sampled, with not a single one observed in the dry season. The rareness of these tadpoles supports the hypothesis that they arrive by accident in the stream, and their normal development takes place in a nest in the leaf litter close to the stream bank, and the tadpoles are washed into the stream after heavy rains.

In contrast, at Montagne d'Ambre National Park we found 40 tadpoles of *G. granulatus* in a stream; similar tadpoles had already been found before without intensive efforts (Glaw & Vences 1994). This supports the idea that for this species completing larval development in the free water of small streams is a very common event.

The observation of direct development in *Gephyromantis* (Blommers-Schlosser 1979; Glaw and Vences 1994) could not be confirmed by our data. Also in *G.* sp. aff. *blanci*, a representative of the subgenus *Gephyromantis* in which males without exception call independent from streams

or other types of free water, and where direct development had been reported by Glaw & Vences (1994) for *G. eiselti*, there was no froglet hatching directly from the egg capsule of terrestrially deposited eggs, with the embryo developing immediately toward a frog morphotype, as in the definition of direct development (Altig & Johnston 1989). In this respect, the observation of Glaw & Vences (1994) should be interpreted with caution. It was based on the observations of a third person who reared a clutch, without photographically documenting the observations. We therefore hypothesize that the development in this species might have been similar to that here described for *G.* sp. aff. *blanci*, and that in fact no direct development occurs in mantellid frogs. The only remaining restriction to this hypothesis is the observation of Blommers-Schlösser (1979) of arboreal eggs from which directly a froglet hatched (purportedly of *G. asper* but almost certainly not belonging to this species; Randrianiaina et al. 2007). The existence of direct development in at least some *Gephyromantis* can therefore not be fully ruled out yet. However, we assume that in fact nidicolous tadpoles (which sometimes become free-swimming in streams) are the only endotrophic developmental type found in *Gephyromantis*. This would be in accordance with the general assessment of Thibaudeau & Altig (1999) that endotrophic developmental modes are invariable within those anuran genera in which they occur.

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Appendix 1

Tadpole descriptions

Boophis englaenderi Glaw & Vences 1994

The following description refers to one tadpole in developmental stage 36 (Field number FGZC 2244; ZSM 623/2008, BL 11.8 mm, TL 25.4 mm) from Marojejy National Park.
In dorsal view, body elliptical (BW 54% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 44% of BL), flatly rounded snout. In lateral view, body depressed (BW 133% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 74% of BL), widely rounded snout. Large eyes (ED 16% of BL), not visible from ventral view, positioned very high (EH 85% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 38% of BL), wide distance between eyes (IOD 74% of BW). Very large rounded nares (ND 5% of BL), marked with a marginal rim provided by a small dorsal projection, positioned very high (NH 83% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 75% of NP) and at eye level (NH 97% of EH), moderately wide distance between nares (IND 44% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 11% of BL), directed posteriorly, visible from dorsal and ventral view and perceptible from lateral view; inner wall free from body, its aperture opens posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 64% of BL), located low on the body (SH 36% of BH) and at the height of the hind limb insertion (SH 54% of HAB). Short medial vent tube (VL 9% of BL), opens directly at the end of the body, not attached to ventral fin. No gland. Short tail (TAL 155% of BL), maximal tail height lower than body height (MTH 90% of BH), tail height at midtail lower than body height and maximal tail height (THM 82% of BH and 92% of MTH), tail height at the beginning of the tail lower than body height (TH 88% of BH). Developed caudal musculature (TMW 54% of BW, TMH 76% of BH, TMH of 87% of TH and 85% of MTH, TMHM 66% of THM and 60% of MTH). Tail muscle reaches tail tip. Very low fins (DF 34% of TMHM, VF 18% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 189% of VF). Dorsal fin originates on the proximal 1/10 of the tail musculature, continues almost parallel to the upper margin of the tail muscle up to the proximal 3/10 where it increases up to its maximal height, then declines towards the tail tip. Ventral fin originates on the 1/10 of the tail musculature, progresses almost parallel to the margin of the tail muscle up to maximal tail height, and then decreases towards the tip of the tail. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 44% of TAL), lateral tail vein visible only on the proximal ¼ of the tail, myosepta visible on the proximal half of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 66% of BH), axis of the tail myotomes is parallel with the axis of the trunk. Tail tip narrowly rounded.
Moderately wide non emarginated generalized oral disk (ODW 56% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Double row of marginal papillae interrupted by a very wide gap on the upper labium (DG 85% of ODW), gap on the lower labium absent; total number of marginal papillae is 128. Thirty-three submarginal papillae (17 in the right and 16 in the left), laterally on lower and upper labia. Short and small conical papillae with protuberance and rounded tip, longest marginal papillae measured 0.12 mm and 0.09 mm for submarginal papillae, papillae not visible from dorsal view. LTRF 6(3-6)/3(1) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Very long A_1 row ($A_{1\ len}$ 90% of ODW). Density of keratodonts varies from 65/mm to 97/mm, $A_{1\ den}$ 74/mm (total 236). Gap in A_2 absent. Row alignment regular, P_1 interrupted. Short keratodonts (0.10 mm), distinguishable from one another in all rows. Distal keratodonts smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath with rounded serrations; moderately wide jaw sheath (JW 46% of ODW) with a very short widely rounded medial convexity (MCL 2% of JW). Lower jaw sheath V-shaped, completely keratinized and partially hidden by the upper jaw sheath. Both jaw sheaths with smooth surface.
Coloration in preservative: Generally dark brown. Brown patches in deep integumental layer (epidermal layer) leaving out laterally a slightly transparent area surrounding the snout and the belly. Dorsally, dark brown spots condensed to form a hexagonal mark above the neocranium, a dark semicircular patch behind each narial opening, and dark patches between the vertebral area and the abdominal region. Snout spotted. Perceivable transversal lines occur between the vertebral area and the abdominal region showing noticeable domino-like structure. The dorsal part of the tail muscle has five dark brown and four light alternating bands. The prominent dark brown band is the extension of the patches between the vertebral area and the abdominal region. Myosepta visible on the dorsal part of the tail. Laterally, jugal area covered by dense dark brown melanophoric patches; flank dorsolaterally identical to the dorsal pattern, abdominal region very dark leaving a distinct transparent spiracle, ventrolaterally whitish, intestinal coils not visible. Tail musculature pale and covered by dark brown spots which condense to form reticulations. Fins transparent, with few brown spots on the dorsal fin, ventral fin free from pigment. Ventrally, oral disk, gular and branchial regions pale; venter more or less transparent, intestinal coils perceptible and regularly spiral shaped.

Boophis englaenderi [Ca45 FGZC 2257]

The following description refers to one tadpole in developmental stage 30 (Field number FGZC 2257, ZSM 1632/2007, BL 10.5 mm, TL 29.5 mm) from Marojejy National Park.
In dorsal view, body elliptical (BW 52% of BL), maximal body width attained between the proximal 3/5 and 4/5 of the body (SBW 66% of BL), flatly rounded snout. In lateral view, body depressed (BW 120% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 71% of BL), widely rounded snout. Moderately large eyes (ED 14% of BL), not visible from ventral view, positioned high (EH 78% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 39% of BL), wide distance between eyes (IOD 69% of BW). Moderately large rounded nares (ND 3% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 75% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 92% of NP) and at eye level (NH 97% of EH), moderately wide distance between nares (IND 50% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 15% of BL), directed posteriorly, visible from ventral view and obvious from lateral view, inner wall free from body, its

aperture opens posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 67% of BL), located low on the body (SH 32% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 58% of HAB). Short medial vent tube (VL 9% of BL), opens directly at the end of the body, not attached to ventral fin. No gland. Short tail (TAL 182% of BL), maximal tail height as high as body height (MTH 101% of BH), tail height at midtail as high as the body height and maximal tail height (THM 100% of BH and MTH), tail height at the beginning of the tail lower than body height (TH 81% of BH). Developed caudal musculature (TMW 66% of BW, TMH 81% of BH, TMH of 100% of TH and 81% of MTH, TMHM 62% of THM and 62% of MTH). Tail muscle reaches tail tip. Very low fins (DF 41% of TMHM, VF 19% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 209% of VF). Dorsal fin originates on the proximal 1/10 of the tail musculature, continues almost parallel to the upper margin of the tail muscle up to the proximal 1/4 where it increases up to the maximal tail height, then continues almost parallel with caudal musculature up to close the tail tip. Ventral fin originates on the 1/10 of the tail musculature, progresses almost parallel to the margin of the tail muscle up to the mid tail, and then increases meticulously to attain its maximal height at about the ¾ of the tail and finally decreases towards the tip of the tail. Maximal tail height located between the proximal 3/5 and 4/5 of the tail (DMTH 62% of TAL), lateral tail vein visible on the proximal 3/4 of the tail, myosepta recognizable visible on the half proximal of the tail musculature, point where the axis of the tail myotomes contacts the body located in the upper half of the body height (HAB 56% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded. Very wide non emarginated generalized oral disk (ODW 84% of BW), bulged laterally, positioned and directed ventrally, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Double row of marginal papillae interrupted by a wide gap on the upper labium (DG 66% of ODW), gap on the lower labium absent; total number of marginal papillae is 175. Ninety-four submarginal papillae, continuous on lower labium and laterally on upper labium. Short and small conical papillae with protuberance and rounded tip, longest marginal papillae measured 0.12 mm and 0.13 mm for submarginal papillae, papillae not visible from dorsal view. LTRF 7(3-7)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Very long A_1 row ($A_{1\ len}$ 82% of ODW). Density of keratodonts varies from 55/mm to 143/mm, $A_{1\ den}$ 80/mm (total 301). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.11 mm), distinguishable from one another in all rows. Distal keratodonts smaller than those in the middle, tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath with rounded serrations, narrow jaw sheath (JW 31% of ODW) with a very short widely pointed medial convexity (MCL 3% of JW). Lower jaw sheath V-shaped, completely keratinized and partially hidden by the upper jaw sheath. Both jaw sheaths with smooth surface.

Coloration in preservative: Generally light brown. Brown patches in deep integumental layers (epidermal layer) leaving out laterally a slightly transparent area surrounding the body. Dorsally, brown spots coalesced to form a hexagonal mark above the neocranium, a brown semicircular patch behind each narial opening, and brown patches between the vertebral area and the abdominal region. Snout spotted. Recognisable transversal lines occur between the vertebral area and the abdominal region showing noticeable domino-like structure. The dorsum of the tail muscle has a more or less zig-zag light area on the half proximal of the tail. The second half part is spotted. Myosepta visible on the dorsal tail. Laterally, jugal area covered by scarce dark brown patches, flank dorsolaterally identical to the dorsal pattern, ventrolaterally more or less transparent, leaving a distinct transparent spiracle over the noticeable intestinal coils. Tail musculature pale and covered by light brown spots which group to form sparse reticulations, dark patch close to the tail tip. Fins transparent, with few brown spots on the dorsal fin, ventral fin free from pigment. Ventrally, oral disk, gular and branchial regions pale, venter dark, intestinal coils not visible.

Variation: the examination of nine other vouchers specimens assigned to *B. englaenderi* [Ca45] (FGZC 2241- ZSM 1499/2007, FGZC 2243- ZSM 527/2008, FGZC 2248- ZSM 1508/2007, FGZC 2250- ZSM 1502/2007, FGZC 2252- ZSM 1503/2007, FGZC 2257- ZSM 529/2008, FGZC 2260- ZSM 530/2008, FGZC 2273- ZSM 1514/2007, FGZC 2275- ZSM 1516/2007) from the same locality show the characteristics of the speciec. Gosner stage 25, BL 6,2-8,9 mm, TL 15,3-20,6 mm, TAL 179-201% of BL, ODW 75-97% of BW, LTRF 7(3-7)/3 except for FGZC 2243- ZSM 527/2008, FGZC 2257- ZSM 529/2008, FGZC 2275- ZSM 1516/2007 which is 6(3-6)/3, MP 92-191, SMP 55-105. These entire tadpole have a light brown Coloration, the spots condenses in some area to fom patches or sparse reticulation.

Boophis andohahela Andreone, Nincheri & Piazza 1995

The following description refers to one tadpole in developmental stage 26 (Field number T 2007-428; ZSM 998/2007, BL 11.8 mm, TL 25.4 mm) from Ranomafana National Park.

In dorsal view, body elliptical (BW 45% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 55% of BL), flatly rounded snout. In lateral view, body depressed (BW 117% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 75 % of BL), widely rounded snout. Moderately large eyes (ED 14% of BL), not visible from ventral view, positioned high (EH 69% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 32% of BL), very wide distance between eyes (IOD 82% of BW). Moderately large rounded nares (ND 3% of BL), marked with a marginal rim and provided by a small dorsal projection, positioned high (NH 57% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 60% of NP) and below eye level (NH 82% of EH), moderately wide distance between nares (IND 50% of IOD), dark spot on the back of the nares absent. Short sinistral spiracle (SL 13% of BL), directed dorsally, perceptible from dorsal and ventral view and visible from lateral view; inner wall free from body, its aperture opens posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 61% of BL), located moderately high on the body (SH 41% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 76% of HAB). Moderately long medial vent tube (VL 11% of BL), opens directly at the end of the body, not attached to ventral fin. No gland. Short tail (TAL 182% of BL), maximal tail height as high as body height (MTH 103% of BH), tail height at midtail as high as the body and maximal tail height (THM 100% of BH and 97% of MTH),

tail height at the beginning of the tail lower than body height (TH 86% of BH). Developed caudal musculature (TMW 63% of BW, TMH 72% of BH, TMH of 70% of TH and 85% of MTH, TMHM 67% of THM and 65% of MTH). Tail muscle reaches tail tip. Very low fins (DF 30% of TMHM, VF 21% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 144% of VF). Dorsal fin originates on the dorsal body-tail junction, increases meticulously up to mid-tail where it remains almost parallel with tail musculature, then declines towards the tail tip. Ventral fin originates on the 1/5 of the tail musculature, increases meticulously up to the mid-tail where it remains almost parallel with tail musculature, then declines towards the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 46% of TAL), lateral tail vein visible only on the proximal half of the tail, myosepta visible on the 3/4 proximal of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 54% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded. Moderately wide non emarginated generalized oral disk (ODW 56% of BW), slightly bulged, positioned and directed ventrally, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Double row of marginal papillae interrupted by a wide gap on the upper labium (DG 70% of ODW), gap on the lower labium absent; total number of marginal papillae is 101. Ninety-four submarginal papillae (46 on the right and 48 on the left), ventrolaterally and laterally on the lower labium and laterally on upper labium. Short and small conical papillae with protuberance and rounded tip, longest marginal submarginal measured 0.08 mm, papillae not visible from dorsal view. LTRF 6(3-6)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Very long A_1 row ($A_{1\ len}$ 88% of ODW). Density of keratodonts varies from 60/mm to 97/mm, $A_{1\ den}$ 67/mm (total 220). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.15 mm), distinguishable from one another in all rows. Distal keratodont smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath with rounded serrations; narrow jaw sheath (JW 36% of ODW) with a very short widely rounded medial convexity (MCL 8% of JW). Lower jaw sheath V-shaped, completely keratinized and partially hidden by the upper jaw sheath. Both jaw sheaths with smooth surface.

Coloration in life: Typically reddish-brown. Body and tail covered by brown spots which condense in some areas to give a dark brown Coloration to the tadpole, the slightly transparent lateral area surrounding the body is noticeable. A hexagonal mark above the neocranium, a dark semicircular patch behind each narial opening and dark domino-like structures between the vertebral area and the abdominal region are obvious. The presence of a white patch behind the hexagonal mark is typical for *B. andreonei* tadpoles. Snout spotted. The dorsum of the tail muscle has four brown and three light alternating bands. The prominent brown band is the extension of the patches between the vertebral area and the abdominal region. Myosepta visible on the tail dorsum. Laterally, jugal area covered by dense brown patches, flank dorsolaterally identical to the dorsal pattern, ventrolaterally silvery, abdominal region very dark leaving a recognisable transparent spiracle. Tail musculature orange covered by sparse brown spots condensed to form patches, their density diminishes towards the tail tip. Fins transparent, with few brown blotches on the dorsal fin, ventral fin free from pigment. Ventrally, oral disk, gular yellowish, branchial region reddish, heart hidden by silvery tissue, venter silver, intestinal coils not visible.

Coloration in preservative: Brown patches in deep integumental layers (epidermal layer) leaving out laterally a slightly transparent area surrounding the snout and the end of the belly. Dorsally, brown spots coalesced to form a hexagonal mark above the neocranium, a brown semicircular patch behind each narial opening and dark patches between the the vertebral area and the abdominal region. A clear area behind the hexagonal mark is obvious. Snout spotted. Recognisable transversal lines occur between the vertebral area and the abdominal region showing noticeable domino-like structure. The dorsum of the tail muscle has some dark and clear alternating bands. Myosepta visible on the dorsum of the tail musculature. Laterally, jugal area between nares and eyes covered by dark brown patches and between eye and spiracle by dark brown scarsed patches, flank dorsolaterally identical to the dorsal pattern, abdominal region very dark leaving a distinct transparent spiracle, ventrolaterally whitish. Intestinal coils not visible. Tail musculature pale and covered by light brown spots which group to form danse reticulations on the half proximal and sparse patches on the half distal of the tail musculature. Fins transparent, with few brown spots on the dorsal fin, ventral fin almost free from pigment. Ventrally, oral disk, gular and branchial regions pale, venter whitish, intestinal coils not visible.

Variation: The examination of six other vouchers specimens assigned to *B. andohahela* (T 60- ZSM 912/2007, T 107- ZSM 1319/2007, T 125- ZSM 1321/2007, T 127- ZSM 1162/2007, T 131- ZSM 1351/2007, T 150- ZSM 0910/2007, T 222- ZSM 566/2007) from the same locality show similarity in the general morphology, only one tadpole (T 222- ZSM 566/2007) has an oral disk with LTRF 5(3-5)/3 and a narrow ventral gap of marginal papillae.

Boophis ankaratra Andreone 1993

The following description refers to one tadpole in developmental stage 28 (Field number ZCMV 4917, ZSM 876/2007, BL 11.3 mm, TL 25.5 mm) from Ranomafana National Park.

In dorsal view, body elliptical (BW 59% of BL), maximal body width attained between the proximal 3/5 and 4/5 of the body (SBW 74% of BL), widely rounded snout. In lateral view, body depressed (BW 129% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 77% of BL), narrowly rounded snout. Large eyes (ED 15% of BL), not visible from ventral view, positioned high (EH 78% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 38% of BL), wide distance between eyes (IOD 60% of BW). Moderately large rounded nares (ND 2% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 67% of BH) dorsally and oriented anterolaterally, situated nearer to eye than to snout (RN 106% of NP) and below eye level (NH 86% of EH), moderately wide distance between nares (IND 54% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 18% of BL), directed posteriorly, visible from ventral view and obvious from lateral view; inner wall free from body and its aperture opens posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 73% of BL), located low on the body (SH 31% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH

53% of HAB). Moderately long medial vent tube (VL 11% of BL), opens directly at the end of the body, not attached to ventral fin. Small dorsolaterally glands present. Short tail (TAL 165% of BL), maximal tail height lower than body height (MTH 90% of BH), tail height at midtail lower than body height and almost equal to maximal tail height (THM 86% of BH and 96% of MTH), tail height at the beginning of the tail lower than body height (TH 84% of BH). Developed caudal musculature (TMW 51% of BW, TMH 68% of BH, TMH of 81% of TH and 76% of MTH, TMHM 53% of THM and 51% of MTH). Tail muscle reaches tail tip. Very low fins (DF 46% of TMHM, VF 43% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 109% of VF). Dorsal fin originates on the dorsal body-tail junction, increases up to its maximal height at the ¾ of the tail, then decreases towards the tail tip. Ventral fin originates on the ventral body-tail junction, increases meticulously up to its maximal height at the ¾ of the tail, and then decreases progressively towards the tip of the tail. Maximal tail height located between the proximal 1/5 and 2/5 of the tail (DMTH 24% of TAL), lateral tail vein not obvious, myosepta visible on the 3/4 proximal of the tail musculature, point where the axis of the tail myotomes contacts the body moderately in the upper half of the body height (HAB 59% of BH), axis of the tail myotomes parallel with the axis of body length. Tail tip narrowly rounded. Wide enlarged oral disk (ODW 73% of BW), bulged laterally, positioned and directed ventrally, maximal width in the middle. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Double row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 51% of ODW), gap on the lower labium absent, total number of marginal papillae is 169. Two hundred and eighteen submarginal papillae, continuous on lower labium and laterally on upper labium. Short and small conical papillae with protuberance and rounded tip, longest marginal papillae measured 0.08 mm and 0.11 mm for submarginal papillae, papillae not visible from dorsal view. LTRF 8(5-8)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\,len}$ 53% of ODW). Density of keratodonts varies from 44/mm to 85/mm, $A_{1\,den}$ 75/mm (total 195). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.12 mm), distinguishable from one another except on A_1 and P_3. Distal keratodonts smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath with finely widely pointed serrations, narrow jaw sheath (JW 33% of ODW) with a short narrowly pointed medial convexity (MCL 10% of JW). Lower jaw sheath U-shaped finely widely pointed serrations, higher than wider, completely keratinized and ribbed.

Coloration in life: Generally yellowish brown. Dorsally, body and tail covered by dense brown spots, the slightly transparent lateral area surrounding the body is discernible. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. Dark domino-like structures between the vertebral area and the abdominal region are recognizable. The dorsum of the tail muscle pigmented, except the area just behind the body-tail junction. Few irregularly dark blotches and silvery spots scattered on the skin. Myosepta visible on the dorsal tail. Laterally, jugal area covered by dense brown patches; flank dorsolaterally identical to the dorsal pattern, ventrolaterally silvery; abdominal region very dark leaving a transparent noticeable spiracle. Tail musculature yellowish, covered by sparse brown spots coalesced to form patches, their density diminishes toward the tail tip. Fins transparent, with few brown blotches on the dorsal fin, ventral fin almost free from pigment. Ventrally, oral disk and gular yellowish, branchial region reddish, heart hidden by silvery tissue; venter silver, intestinal coils not visible.

Coloration in preservative: Brown spots in deep integumental layers (epidermal layer) leaving out laterally a slightly transparent area surrounding the snout and the end of the belly. Dorsally, light brown speckles in deep integumental layers coalesced to form a hexagonal mark above the neocranium, a brown semicircular patch behind each narial opening and dark patches between the the vertebral area and the abdominal region. Darker brow spots on the dermal layer coalesced to form sporadic patches surrounding the snout on the body and tail dorsum. Recognisable transversal lines occur between the vertebral area and the abdominal region showing noticeable domino-like structure. Myosepta visible on the dorsum of the tail musculature. Laterally, light brown spots in deep integumental layer coalesce on the jugal area between nares and eyes and between eye and spiracle. A darker tegumental spots group to form scaterred patches surrounding the snout and on the flank dorsolaterally, abdominal region very dark leaving a noticeable transparent spiracle. Intestinal coils not visible. Tail musculature pale and covered by light brown spots which fuse to form sparse reticulations leaving some clear areas in between. Density of reticulation dinishes toward tail tip. Fins transparent, with sporadic brown blotches on the dorsal fin, and close to the tail tip for the ventral one. Ventrally, oral disk, gular and branchial regions pale, venter whitish, intestinal coils not visible.

Variation: Two other voucher specimens assigned to *B. ankaratra* (FGMV 2003-1698 - ZSM 816/2004, ZCMV 3803- ZSM 168/2008) present the typical characters of the species.

Boophis schuboeae Glaw & Vences 2002

The following description refers to one tadpole in developmental stage 36 (Field number FGMV 2002-1800, ZSM 978/2004, BL 12.1 mm, TL 25.5 mm) from Ranomafana National Park.

In dorsal view, body elliptical (BW 57% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 48% of BL), widely rounded snout. In lateral view, body depressed (BW 144% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 67% of BL), narrowly rounded snout. Large eyes (ED 15% of BL), not visible from ventral view, positioned high (EH 73% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 33% of BL), wide distance between eyes (IOD 65% of BW). Moderately large rounded nares (ND 2% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 64% of BH) dorsally and oriented anterolaterally, situated at the mid-distance between the eye and the snout (RN 103% of NP) and below eye level (NH 87% of EH), moderately wide distance between nares (IND 48% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 19% of BL), directed posteriorly, visible from dorsal and ventral views and obvious from lateral view; inner wall free from body and its aperture opens posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 76% of BL), located moderately high on the body (SH 41% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 64% of HAB). Short medial vent tube (VL 9% of BL), opens directly at the end

of the body, not attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 163% of BL), maximal tail height lower than body height (MTH 94% of BH), tail height at midtail lower than body height and as high as maximal tail height (THM 93% of BH and 100% of MTH), tail height at the beginning of the tail lower than body height (TH 69% of BH). Developed caudal musculature (TMW 54% of BW, TMH 69% of BH, TMH of 100% of TH and 74% of MTH, TMHM 59% of THM and 59% of MTH). Tail muscle reaches tail tip. Very low fins (DF 46% of TMHM, VF 24% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 109% of VF). Dorsal fin originates on the proximal 3/10 of the tail musculature, increases abruptly up to the midtail, then progresses almost parallel with the caudal musculature until decreasing just close to the tail tip. Ventral fin originates on the proximal 4/10 of the tail musculature, remains almost parallel with the dorsal fin until decreasing just close to the tail tip. Maximal tail height located at midtail (DMTH 50% of TAL), lateral tail vein visible on the 1/3 proximal of the tail, myosepta recognizable all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 64% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded. Wide enlarged oral disk (ODW 74% of BW), bulged laterally, positioned and directed ventrally, maximal width in the centre. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Double row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 59% of ODW), gap on the lower labium absent; total number of marginal papillae is 148. One hundred and ninety submarginal papillae, continuous on lower labium and laterally on upper labium. The lateral area where the oral disk folds is free from papillae. Short and small conical papillae with protuberance and rounded tip, longest marginal and submarginal papillae measured 0.11 mm, papillae not visible from dorsal view. LTRF 8(5-8)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\ len}$ 49% of ODW). Density of keratodonts varies from 48/mm to 115/mm, $A_{1\ den}$ 115/mm (total 285). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.12 mm), only keratodonts in the middle of A_4 to A_8 distinguishable from one another. Distal keratodont very small than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath with finely widely pointed serrations; narrow jaw sheath (JW 33% of ODW) with a short narrowly pointed medial convexity (MCL 7% of JW). Lower jaw sheath U-shaped with finely widely pointed serrations, higher than wide, completely keratinized and ribbed.

Coloration in life: Generally yellowish brown. Dorsally, body covered by brown dense spots, the slightly transparent lateral area surrounding the body is perceivable.. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. Dark domino-like structures between the vertebral area and the abdominal region are recognizable. The dorsum of the tail muscle has up to four light and three dark alternating bands. The prominent light band is a clear area just behind the dorsal body tail-junction, sometimes not obvious. The second band which is a dark one can extend until midtail and beyond. Myosepta visible on the dorsal tail. Few irregularly dark blotches and silvery spots scattered on the skin, mainly on the body. Laterally, jugal area covered by dense brown patches, below the eye generally reddish; flank dorsolaterally identical to the dorsal pattern, ventrolaterally silvery; abdominal region very dark leaving a recognizable transparent spiracle. The distal part of the tail sometimes with a contrasting orange coloration. Generally, the tail muscle is provided by three light and two dark alternating bands..The dark band is formed by coalesced brown spots, which are generally dense on the upper part of the tail muscle. Fins transparent, with few brown blotches on the dorsal fin, ventral fin almost free from pigment. Ventrally, oral disk and gular yellowish, branchial region reddish, heart hidden by silvery tissue; venter silver, intestinal coils not visible.

Coloration in preservative: Brown spots in deep integumental layers (epidermal layer) leaving out laterally a slightly transparent area surrounding the snout and the end of the belly. Dorsally, light brown speckles in deep integumental layers coalesced to form a hexagonal mark above the neocranium, a brown semicircular patch behind each narial opening and dark patches between the the vertebral area and the abdominal region. Darker brow spots on the dermal layer coalesced to form sarse patches surrounding the snout on the body and tail dorsum. Recognisable transversal lines occur between the vertebral area and the abdominal region showing noticeable domino-like structure. Up to four light and three dark alternating bands are visible on the dorsum of the tail musculature. Laterally, light brown spots in deep integumental layer congregate on the jugal area. Darker tegumental coalesced spots form discipated patches surrounding the snout and on the flank dorsolaterally, abdominal region very dark leaving a noticeable transparent spiracle, intestinal coils not visible. Tail musculature pale and covered by brown spots which merge to form dark bands. The light bands are almost free from pigments. Fins transparent, with dispersed brown blotches on the dorsal fin, ventral fin usually free from pigment. Ventrally, oral disk, gular and branchial regions pale, venter whitish, intestinal coils not visible.

Variation: Six other vouchers specimens assigned to *B. schuboeae* (Tad 2004-780- ZSM 1339/2004, Tad 2004-797- ZSM 1356-2004, T 09/980- ZSM 743/2008, T 09/968- ZSM 739/2008, T 09/971- ZSM 740/2008, T 09/998- ZSM 749/2008) from the same locality have the typical coloration pattern and the oral disk configuration of the species.

Boophis albipunctatus Glaw & Thiesmeier 1993

The following description refers to one tadpole in developmental stage 25 (Field number ZCMV 4946, ZSM 82/2008, BL 7.5 mm, TL 15.5 mm) from Ambohitsara-Tsitolaka.

In dorsal view, body elliptical (BW 52% of BL), maximal body width attained between the proximal 3/5 and 4/5 of the body (SBW 67% of BL), widely rounded snout. In lateral view, body depressed (BW 139% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 79% of BL), narrowly rounded snout. Moderately large eyes (ED 13% of BL), not visible from ventral view, positioned very high (EH 80% of BH) dorsally and directed dorsolaterally, situated between the proximal 4/10 and 5/10 of the body (SE 44% of BL), wide distance between eyes (IOD 69% of BW). Large rounded nares (ND 3% of BL), marked with a marginal rim provided by a small dorsal projection, positioned very high (NH 83% of BH) dorsally and oriented anterolaterally, situated nearer to eye than to snout (RN 120% of NP) and above eye level (NH 108% of EH), moderately wide distance between nares (IND 52% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 16% of BL), directed posteriorly, visible from dorsal and ventral views and obvious from lateral view; inner wall free

from body and its aperture opens laterally instead of posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 74% of BL), located moderately high on the body (SH 43% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 76% of HAB). Moderately long medial vent tube (VL 11% of BL), opens directly at the end of the body, not attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 156% of BL), maximal tail height as high as the body (MTH 100% of BH), tail height at midtail as high as the body and lower than maximal tail height (THM 102% of BH and 93% of MTH), tail height at the beginning of the tail lower than body height (TH 86% of BH). Developed caudal musculature (TMW 52% of BW, TMH 68% of BH, TMH of 79% of TH and 62% of MTH, TMHM 45% of THM and 41% of MTH). Tail muscle reaches tail tip. Low fins (DF 72% of TMHM, VF 52% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 137% of VF). Dorsal fin originates on just behind the dorsal body-tail junction, augments regularly up to the midtail, and then remains straight until decreasing just close to the tail tip. Ventral fin originates just behind the ventral body-tail junction, augments meticulously up to the midtail, and then remains straight until decreasing just close to the tail tip. Maximal tail height located between the proximal 1/5 and 2/5 of the tail (DMTH 34% of TAL), lateral tail vein unperceivable, myosepta recognizable all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 57% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Very wide enlarged oral disk (ODW 84% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Double row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 41% of ODW), gap on the lower labium absent; total number of marginal papillae is 174. Three hundred and sixty eight submarginal papillae, continuous on lower labium and laterally and dorsolaterally on upper labium. Very short and small conical papillae with protuberance and rounded tip, longest marginal and submarginal papillae measured 0.07 mm, papillae not visible from dorsal view. LTRF 7(5-7)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\ len}$ 51% of ODW). Density of keratodonts varies from 46/mm to 109/mm, $A_{1\ den}$ 102/mm (total 171). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Short keratodonts (0.07 mm), only keratodonts on A_1, A_2 and P_3 distinguishable from one another. Distal keratodont much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath with widely rounded serrations; narrow jaw sheath (JW 29% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in life: Generally yellowish brown. Dorsally, body uniformly dark, the slightly transparent lateral area surrounding the body is evident. The hexagonal mark above the neocranium and the dark semicircular patch behind each narial opening are not obvious. The dorsum of the tail muscle has some light patches. Some silvery spots scattered on the skin, mainly on the body. Laterally, jugal area covered by sporadic brown blotches below the eye generally reddish; flank dorsolaterally identical to the dorsal pattern, ventrolaterally silvery; abdominal region silvery leaving a recognizable transparent spiracle. Tail musculature commonly yellowish with sparsed reticulations. Fins transparent and free from pigment. Ventrally, oral disk and gular yellowish, branchial region reddish, heart not hidden by silvery tissue; venter silver, intestinal coils not visible.
Coloration in preservative: Typically whitish. Dorsally, body covered by sparse brown spots in deep integumental layers leaving an obvious transparent lateral area surrounding the body, darker brown spots scattered on the skin. The hexagonal mark above the neocranium is noticeable, but the dark semicircular patch behind each narial opening is sometimes indiscernible. The dark domino-like structures between the vertebral area and the abdominal region is noticeable and the dorsolateral glands are obvious. The dorsum of the tail muscle seems to present bands. Laterally, jugal area and flank dorsolaterally spotted, ventrolaterally free of pigment; abdominal region very dark leaving an obvious transparent spiracle, intestinal coil invisible. Tail musculature pale, provided by brown spots which coalesced to form scattered patches or reticulations. The bands seen from dorsal view are just a lack of pigmentation on some area of the dorsal side of the tail muscle. Ventrally, oral disk, gular and branchial regions pale, venter dark, intestinal coils not visible.
Variation: One other voucher tadpole of *B. albipunctatus* (ZCMV 4942 ZSM 78/2008) from the same locality is very similar to the described voucher specimen.

Boophis sibilans Glaw & Thiesmeier 1993

The following description refers to one tadpole in developmental stage 29 (Field number FGZC 2956, ZSM 1631/2007, BL 11 mm, TL 26 mm) from Marojejy National Park.
In dorsal view, body elliptical (BW 52% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 48% of BL), widely rounded snout. In lateral view, body depressed (BW 124% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 76% of BL), narrowly rounded snout. Moderately large eyes (ED 13% of BL), not visible from ventral view, positioned high (EH 77% of BH) dorsally and directed dorsolaterally, situated between the proximal 4/10 and 5/10 of the body (SE 43% of BL), wide distance between eyes (IOD 78% of BW). Large rounded nares (ND 3% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 77% of BH) dorsally and oriented anterolaterally, situated nearer to eye than to snout (RN 108% of NP) and at eye level (NH 100% of EH), moderately wide distance between nares (IND 47% of IOD), dark spot on the back of the nares present. Moderately long sinistral spiracle (SL 20% of BL), directed posteriorly, visible from dorsal and ventral view and obvious from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 75% of BL), located moderately high on the body (SH 44% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 82% of HAB). Moderately long medial vent tube (VL 11% of BL), opens directly at the end of the body, not attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 184% of BL), maximal tail height higher than body height (MTH 113% of BH), tail height at midtail higher than body height and as high as maximal tail height (THM 113% of BH and 100% of MTH), tail height at the beginning of the tail lower than body height (TH 92% of BH). Developed caudal musculature (TMW 59% of BW, TMH 75% of BH, TMH of 83% of TH and 66% of MTH, TMHM 50% of THM and 50% of MTH). Tail muscle reaches tail tip. Low fins (DF 56% of TMHM, VF 43% of MTHM), dorsal fin

higher than ventral fin at midtail (DF 130% of VF). Dorsal fin originates just behind the dorsal body-tail junction, progresses almost parallel with the upper margin of tail musculature up to 1/5 of the tail where it increases gradually up to midtail, then remains straight until decreasing just close to the tail tip. Ventral fin originates just behind the ventral body-tail junction, augments meticulously up to the midtail, and then remains straight until decreasing just close to the tail tip. Maximal tail height located at midtail (DMTH 50% of TAL), lateral tail vein unperceivable, myosepta recognizable all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 53% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Very wide enlarged oral disk (ODW 80% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Double row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 48% of ODW), gap on the lower labium absent; total number of marginal papillae is 177. Two hundred and forty five submarginal papillae, continuous on lower labium and laterally and dorsolaterally on upper labium. Very short and small conical papillae with protuberance and rounded tip, longest marginal and submarginal papillae measured 0.08 mm, papillae not visible from dorsal view. LTRF 7(5-7)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\ len}$ 50% of ODW). Density of keratodonts varies from 47/mm to 104/mm, $A_{1\ den}$ 104/mm (total 241). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.13 mm), only keratonts on P_1 and P_2 distinguishable from one another. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath with widely rounded serrations; narrow jaw sheath (JW 37% of ODW). Lower jaw sheath V-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.

Coloration in life: Generally yellow brownish. Dorsally, body covered by brown spots, the slightly transparent lateral area surrounding the body is evident. The hexagonal mark above the neocranium and the dark semicircular patch behind each narial opening are obvious. The dark domino-like structures between the vertebral area and the abdominal region are recognizable. The dorsum of the tail muscle has up to six light and five dark alternating bands. The prominent light band is a clear area just behind the dorsal body tail-junction, sometimes not really obvious. Myosepta visible on the tail dorsum. Few irregularly dark blotches and silvery spots scattered on the skin, mainly on the body. Laterally, jugal area spotted, below the eye generally reddish; flank dorsolaterally identical to the dorsal pattern, ventrolaterally silvery; abdominal region very dark leaving a noticeable transparent spiracle. Tail musculature yellowish. Generally, the tail muscle is provided by an equal number of dark and light alternating sections. The first lighter band seen from dorsal view is caused by the absence of pigment on the dorsal side of the tail muscle just behind the dorsal body-tail junction. Brown spots condensed to form distinct irregular vast dark patches on tail muscle. Usually the inner part of the patches is free from pigment. Ventral side of the tail muscle free from pigments. Fins transparent, with few dots. Ventrally, oral disk yellowish, gular and branchial regions reddish, heart hidden by silvery tissue; venter silver, intestinal coils not visible.

Coloration in preservative: Dorsally, light brown speckles in deep integumental layers leaving an obvious transparent lateral area surrounding the body. Speckles coalesced to form a hexagonal mark above the neocranium. Darker brow spots on the dermal layer coalesced to form scarse patches surrounding the snout on the body and tail dorsum. The semicircular patch behind each narial opening is obvious. Transversal lines between the vertebral area and the abdominal region indiscernible. Up to six light and five dark alternating bands are visible on the dorsum of the tail musculature. Laterally, light brown spots in deep integumental layer congregate on the jugal area. Darker tegumental fused spots form discipated patches surrounding the snout and on the flank dorsolaterally, abdominal region very dark leaving a perceptible transparent spiracle, intestinal coils not visible. Tail musculature pale and covered by brown spots which merge to form dark spots. The spots are separated by clear unpigmented area and their inner part is normally free from pigment. Fins transparent and usually free from pigment. Ventrally, oral disk, gular and branchial regions pale, venter whitish, intestinal coils not visible.

Variation: One other voucher tadpole of *B. schuboeae* from Andasibe (LR 269 - ZSM 557/2004) and other one from An'Ala (ZCMV 3450 - ZSM 1754/2007) have the characteristics of the species.

Boophis luciae Glaw, Köhler, de la Riva, Vieites & Vences 2010

The following description refers to one tadpole in developmental stage 36 (Field number ZCMV 5146, ZSM 730/2007, BL 10.4 mm, TL 22.2 mm) from Ranomafana National Park.

In dorsal view, body elliptical (BW 46% of BL), maximal body width attained between the proximal 1/5 and 2/5 of the body (SBW 39% of BL), widely rounded snout. In lateral view, body depressed (BW 141% of BH), maximal body height attained between the proximal 2/5 and 3/5 of the body (SBH 49% of BL), narrowly rounded snout. Large eyes (ED 17% of BL), not visible from ventral view, positioned high (EH 70% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 38% of BL), wide distance between eyes (IOD 79% of BW). Large rounded nares (ND 3% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 69% of BH) dorsally and oriented anterolaterally, situated almost in mid-distance between the eye and the snout (RN 105% of NP) and at eye level (NH 97% of EH), moderately wide distance between nares (IND 51% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 12% of BL), directed posteriorly, visible from dorsal and ventral views and obvious from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 65% of BL), located moderately high on the body (SH 17% of BH) and at the height of the hind limb insertion (SH 31% of HAB). Moderately long medial vent tube (VL 14% of BL), opens directly at the end of the body, not attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 167% of BL), maximal tail height higher than body height (MTH 110% of BH), tail height at midtail higher than body height and as high as maximal tail height (THM 108% of BH and 98% of MTH), tail height at the beginning of the tail lower than body height (TH 86% of BH). Developed caudal musculature (TMW 56% of BW, TMH 86% of BH, TMH of 100% of TH and 79% of MTH, TMHM 60% of THM and 59% of MTH). Tail muscle reaches tail tip. Very low fins (DF 37% of TMHM, VF 32% of MTHM), dorsal fin higher than ventral fin at midtail (DF

111% of VF). Dorsal fin originates just behind the dorsal body-tail junction, progresses almost parallel with the upper margin of tail musculature up to 1/5 of the tail where it increases gradually up to its maximal height at ¾ of the tail, and then declines meticulously until decreasing abruptly towards the tail tip. Ventral fin originates on the 1/5 of the tail musculature, augments gradually up to the midtail, and then remains almost straight until decreasing just close to the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 45% of TAL), lateral tail vein recognizable on the proximal half of the tail, myosepta visible almost all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 56% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Very wide enlarged oral disk (ODW 91% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Double row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 55% of ODW), gap on the lower labium absent; total number of marginal papillae is 152. Two hundred and ninety seven submarginal papillae, continuous on lower labium and laterally and dorsolaterally on upper labium. Short and small conical papillae with protuberance and rounded tip, longest marginal papillae measured 0.14 mm 0.10 mm for submarginal ones, papillae not visible from dorsal view. LTRF 7(5-7)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\ len}$ 56% of ODW). Density of keratodonts varies from 51/mm to 102/mm, $A_{1\ den}$ 102/mm (total 263). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.15 mm), only keratonts distinguishable from one another except on A_1, A2 and P_3. Distal keratodont much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath with widely rounded serrations; narrow jaw sheath (JW 33% of ODW). Lower jaw sheath V-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.

Coloration in life: Generally yellowish brownish. Dorsal sides of head and trunk covered by brown spots, the slightly transparent lateral area surrounding the body is perceiveble. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. The dark domino-like structures between the vertebral area and the abdominal region are recognizable. The dorsum of the tail muscle has light and dark alternating bands. The prominent light band is a clear area just behind the dorsal body tail-junction, myosepta visible on the tail dorsum. Few irregularly dark blotches and vast reticulation of silvery pigments scattered on the body dorsum. Laterally, jugal area spotted and sometimes blotched, below the eye generally reddish; flank dorsolaterally identical to the dorsal pattern, ventrolaterally silvery; abdominal region very dark leaving a noticeable transparent spiracle. Tail musculature yellowish. Generally, the tail muscle has an equal number of dark and light alternating sections. The first lighter band seen from dorsal view is sometimes not obvious. Brown spots condensed to form distinct irregular vast dark spots, which are always connected one another by a small dark bridge, making an interrupted light band. Usually the inner part of the patches is free from pigment. Ventral side of the tail muscle free from pigments. Fins transparent and free from pigments. Ventrally, oral disk yellowish, gular and branchial regions reddish, heart hidden by silvery tissue; venter silver, intestinal coils not visible.

Coloration in preservative: Dorsally, light brown dots in deep integumental layers leaving an obvious transparent lateral area surrounding the body. Dots coalesced to form a hexagonal mark above the neocranium and a semicircular patch behind each narial opening. Fused darker brow spots form dispersed patches on the body and tail dorsum. Transversal lines between the vertebral area and the abdominal region discernible showing noticeable domino-like structure. Up to six light and five dark alternating bands are visible on the dorsum of the tail musculature. Laterally, light brown speckles spread surrounding the snout; darker spots in deep integumental layer congregate on the jugal area and on the flank dorsolaterally, abdominal region very dark leaving a perceptible transparent spiracle, intestinal coils not visible. Tail musculature pale and covered by brown spots which merge to form dark spots. The spots are connected together sometime just with a thick dark bridge and their inner part is mostly free from pigment. Fins transparent and usually free from pigment. Ventrally, oral disk, gular and branchial regions pale, venter whitish, intestinal coils not visible.

Variation: Ten voucher specimens assigned to *B. luciae* (T 176- ZSM 792/2007, T 177- ZSM 593/2007, T 178- ZSM 541/2007, T 179- ZSM 976/2007, T 224- ZSM 264/2007, T 430- ZSM 274/2007, ZCMV 3619- ZSM 1587/2006, ZCMV 3631- ZSM 1588/2006, ZCMV 3686- ZSM 634/2008, ZCMV 4024- ZSM 0688/2007) from the same locality are identical to the described voucher specimen.

Boophis sambirano Vences & Glaw 2005

The following description refers to one tadpole in developmental stage 25 (Field number FG/MV 2002.1902, ZSM 672/2004, BL 6.5 mm, TL 12.7 mm) from the Camp Norbert in the Special Reserve of Manongarivo.

In dorsal view, body elliptical (BW 63% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 57% of BL), widely rounded snout. In lateral view, body depressed (BW 132% of BH), maximal body height attained between on distal 1/5 of the body (SBH 81% of BL), broadly rounded snout. Moderately large eyes (ED 14% of BL), not visible from ventral view, positioned very high (EH 86% of BH) dorsally and directed dorsolaterally, situated at midbody (SE 49% of BL), moderately wide distance between eyes (IOD 59% of BW). Large rounded nares (ND 4% of BL), marked with a marginal rim provided by a small dorsal projection, positioned very high (NH 84% of BH) dorsally and oriented anterolaterally, situated nearer to eye than to snout (RN 159% of NP) and at eye level (NH 98% of EH), moderately wide distance between nares (IND 50% of IOD), dark spot on the back of the nares present. Very short sinistral spiracle (SL 16% of BL), directed posterodorsally, visible from ventral view and perceptible from lateral view; inner wall free from body and its aperture opens posteriorly, elliptical opening, situated on the distal 1/5 of the body (SS 84% of BL), located low on the body (SH 35% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 62% of HAB). Short dextral vent tube (VL 8% of BL), inner wall absent, attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 156% of BL), maximal tail height lower than body height (MTH 67% of BH), tail height at midtail lower than body height and maximal tail height (THM 67% of BH and 96% of MTH), tail height at the beginning of the tail lower than body height (TH 67% of BH). Developed caudal musculature (TMW 43% of BW, TMH 65% of BH, TMH of 96% of TH and 96% of MTH, TMHM 63% of

THM and 63% of MTH). Tail muscle reaches tail tip. Very low fins (DF 31% of TMHM, VF 22% of MTHM), dorsal fin higher than ventral fin at midtail (DF 154% of VF). Dorsal fin originates on the dorsal body-tail junction, progresses almost parallel with the upper margin of tail musculature up to 1/4 of the tail where it increases abruptly up to its maximal height at mid tail, and then continues straight until decreasing just close to the tail tip. Ventral fin originates on the 1/10 of the tail musculature, increases gradually up to its maximal height at mid-tail, and then decreases rapidly towards the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 43% of TAL), lateral tail vein visible all along the tail, myosepta obvious all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 57% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Very wide enlarged oral disk (ODW 95% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Oral disk rounded shaped when open. Single row of marginal papillae, gap on upper labium and the lower labium absent; total number of marginal papillae is 248. Two hundred and fifty five submarginal papillae, continuous on the lower labium and laterally on the upper labium, the lateral area where the oral disk folds is free from papillae. Very short and small conical marginal papillae with rounded tip, longest marginal papillae measured 0.09 mm 0.11 mm for submarginal ones, papillae visible from dorsal view. LTRF 9(6-9)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Short A_1 row ($A_{1\ len}$ 30% of ODW). Density of keratodonts varies from 58/mm to 175/mm, $A_{1\ den}$ 112/mm (total 163). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Short keratodonts (0.06 mm), distinguishable from one another. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath absent; narrow jaw sheath (JW 40% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in preservative: Generally dark brown. Dark brown spots positioned in deep integumental layers, separated from a (possibly epidermal) transparent outer skin layer, leaving out laterally a conspicuous transparent area on the 2/3 proximal of the body, the abdominal region has no lateral transparent area. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. The dark domino-like structures between the vertebral area and the abdominal region are recognizable. The abdominal region is very dark. The transparent area around the snout is spotted. The dorsum of the tail muscle is spotted, density of spots diminishes towards tail tip. Myosepta visible on the tail dorsum. Laterally, jugal area covered by dense dark brown spots; abdominal region very dark leaving out a transparent discernible spiracle, intestinal coils invisible. Tail musculature pale and covered by dark brown spots which are more dense on the proximal half. The distal half has less spots. Fins transparent, with few brown spots on the dorsal fin, ventral fin free from pigment. Ventrally, oral disk, gular and branchial regions pale; venter very dark, intestinal coils not visible.
Variation: many non-voucher specimens of the same series are identical to the voucher specimen.

Boophis mandraka [Ca38 Vieites et al. 2009]

The following description refers to one tadpole in developmental stage 26 (Field number ZCMV 4261, ZSM 456/2007, BL 7.6 mm, TL 15.8 mm) from Ranomafana National Park.
In dorsal view, body elliptical (BW 61% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 56% of BL), widely rounded snout. In lateral view, body depressed (BW 132% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 63% of BL), narrowly rounded snout. Large eyes (ED 15% of BL), not visible from ventral view, positioned high (EH 77% of BH) dorsally and directed dorsolaterally, situated at midbody (SE 49% of BL), wide distance between eyes (IOD 59% of BW). Large rounded nares (ND 3% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 77% of BH) dorsally and oriented anterolaterally, situated nearer to eye than to snout (RN 125% of NP) and at eye level (NH 101% of EH), wide distance between nares (IND 61% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 17% of BL), directed posteriorly, visible from dorsal and ventral view and obvious from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, elliptical opening, situated on the proximal ¼ of the body (SS 83% of BL), located low on the body (SH 25% of BH) and at the height of the hind limb insertion (SH 47% of HAB). Short dextral vent tube (VL 8% of BL), inner wall absent, attached to ventral fin. Large dorsolateral glands present. Very short tail (TAL 146% of BL), maximal tail height lower than body height (MTH 89% of BH), tail height at midtail lower than body height and maximal tail height (THM 54% of BH and 70% of MTH), tail height at the beginning of the tail lower than body height (TH 77% of BH). Moderately developed caudal musculature (TMW 37% of BW, TMH 54% of BH, TMH of 70% of TH and 61% of MTH, TMHM 46% of THM and 41% of MTH). Tail muscle reaches tail tip. Low fins (DF 83% of TMHM, VF 37% of MTHM), dorsal fin higher than ventral fin at midtail (DF 232% of VF). Dorsal fin originates on the dorsal body-tail junction, progresses almost parallel with the upper margin of tail musculature up to 1/5 of the tail where it increases gradually up to its maximal height at midtail, and then declines continuously towards the tail tip. Ventral fin originates on the dorsal body-tail junction, progresses almost parallel with the lower margin of the tail musculature up until decreasing just close to the tail tip. Maximal tail height located between the proximal 1/5 and 2/5 of the tail (DMTH 45% of TAL), lateral tail vein unperceivable, myosepta visible almost all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 53% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Very wide enlarged oral disk (ODW 90% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Single row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 42% of ODW), gap on the lower labium absent; total number of marginal papillae is 273. Two hundred and twenty nine submarginal papillae, continuous on lower labium and laterally and dorsolaterally on upper labium. Very short and small conical papillae with protuberance and rounded tip, longest marginal papillae measured 0.08 mm 0.09 mm for submarginal ones, papillae visible from dorsal view. LTRF 8(6-8)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Short A_1 row ($A_{1\ len}$ 39% of ODW). Density of keratodonts varies

from 34/mm to 143/mm, $A_{1\ den}$ 102/mm (total 166). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.10 mm), not distinguishable from one another. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Upper jaw sheath absent but its trace still evident; narrow jaw sheath (JW 32% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in life: Typically yellowish. Dorsally, the 2/3 proximal half of the body almost free from pigments, 1/3 distal very dark, the slightly transparent lateral area surrounding the body is evident. A hexagonal mark above the neocranium and dark semicircular patch behind each narial opening are noticeable, dark domino-like structures between the vertebral area and the abdominal region are perceivable and the dorsolateral glands are obvious. Tail finely speckled. Irregular silvery blotches scattered on the skin, mainly on the body. Laterally, free from pigments; flank dorsolaterally identical to the dorsal pattern, ventrolaterally silvery; abdominal region very dark leaving a noticeable transparent spiracle. Tail musculature yellowish with speckles marking the myosepta and the dorsal and ventral margins of tail muscle. Fins transparent and free from pigments. Ventrally, oral disk, gular, branchial regions pale, venter dark, intestinal coils not visible.
Coloration in preservative: Typically whitish. Dorsally, the 2/3 proximal half of the body almost free from pigments, 1/3 distal very dark, the slightly transparent lateral area surrounding the body is imperceptible as the tadpole is whitish. The hexagonal mark above the neocranium is noticeable and the dark semicircular patch behind each narial opening is visibleble. The dark domino-like structures between the vertebral area and the abdominal region are perceivable and the dorsolateral glands are obvious. Laterally, jugal area speckled, flank dorsolaterally spotted, ventrolaterally whitish; abdominal region very dark leaving an obvious transparent spiracle, intestinal coil invisible. Tail musculature whitish, provided dissipated spots. Fins sporadically spotted. Ventrally, oral disk, gular and branchial regions pale, venter dark, intestinal coils not visible.

Boophis mandraka [Ca46 ZCMV 3479]

The following description refers to one tadpole in developmental stage 25 (Field number ZCMV 3479, ZSM 1784/2007, BL 6.8 mm, TL 14.3 mm) from An'Ala.
In dorsal view, body elliptical (BW 52% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 53% of BL), widely rounded snout. In lateral view, body depressed (BW 122% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 67% of BL), narrowly rounded snout. Large eyes (ED 15% of BL), not visible from ventral view, positioned high (EH 75% of BH) dorsally and directed dorsolaterally, situated at midbody (SE 49% of BL), wide distance between eyes (IOD 72% of BW). Large rounded nares (ND 3% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 77% of BH) dorsally and oriented anterolaterally, situated nearer to eye than to snout (RN 194% of NP) and at eye level (NH 101% of EH), moderately wide distance between nares (IND 53% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 13% of BL), directed posterodorsally, visible from ventral view and perceptible from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 72% of BL), located low on the body (SH 34% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 59% of HAB). Short dextral vent tube (VL 7% of BL), inner wall absent, attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 159% of BL), maximal tail height higher than body height (MTH 107% of BH), tail height at midtail higher than body height and as high as maximal tail height (THM 107% of BH and 100% of MTH), tail height at the beginning of the tail lower than body height (TH 82% of BH). Moderately developed caudal musculature (TMW 52% of BW, TMH 58% of BH, TMH of 71% of TH and 54% of MTH, TMHM 52% of THM and MTH). Tail muscle reaches tail tip. Very low fins (DF 58% of TMHM, VF 35% of MTHM), dorsal fin higher than ventral fin at midtail (DF 166% of VF). Dorsal fin originates on the dorsal body-tail junction, progresses almost parallel with the upper margin of tail musculature up to 1/4 of the tail where it increases gradually up to its maximal height at midtail, and then declines continuously towards the tail tip. Ventral fin originates on the dorsal body-tail junction, increases meticulously up to midtail, and then progresses almost parallel with the lower margin of the tail musculature before it decreases towards the tail tip. Maximal tail height located at mid tail (DMTH 50% of TAL), lateral tail vein visible all along the tail, myosepta obvious on the proximal half of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 58% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Wide enlarged oral disk (ODW 101% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Single row of marginal papillae interrupted by a very narrow gap on the upper labium (DG 14% of ODW), gap on the lower labium absent; total number of marginal papillae is 291. One hundred and ninety three submarginal papillae, continuous on lower labium and laterally and dorsolaterally on upper labium. Very short and small conical marginal papillae, submarginal papillae larger than marginal ones, papillae with rounded tip, longest marginal papillae measured 0.04 mm 0.07 mm for submarginal ones, papillae visible from dorsal view. LTRF 8(6-8)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Short A_1 row ($A_{1\ len}$ 21% of ODW). Density of keratodonts varies from 62/mm to 128/mm, $A_{1\ den}$ 128/mm (total 95). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Short keratodonts (0.07 mm), not distinguishable from one another. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Upper jaw sheath absent but its trace still evident; narrow jaw sheath (JW 31% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in preservative: Generally dark brown. Dark brown spots in deep integumental layers leaving out laterally a conspicuous transparent area. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. The dark domino-like structures between the vertebral area and the abdominal region are recognizable. The abdominal region is very dark. The transparent area around the snout is spotted. The dorsum of the tail muscle is spotted, density of spots diminishes toward tail tip. Myosepta visible on the tail dorsum. Laterally, jugal area covered by dense dark brown spots; flank dorsolaterally identical to the dorsal pattern, abdominal region very dark leaving a transparent discernible

spiracle, intestinal coils invisible. Tail musculature pale and covered by dark brown spots which group mainly on the dorsolateral side of the proximal half. The distal half has less spots. Fins transparent, with few brown spots on the dorsal fin, ventral fin free from pigment. Vessel traces are conspicuous on fins. Ventrally, oral disk, gular and branchial regions pale; venter very dark, intestinal coils not visible.

Boophis sambirano [Ca47 ZCMV 13105]

The following description refers to one tadpole in developmental stage 27 (Field number ZCMV 13105, ZSM 0482/2010, BL 13,5 mm, TL 27,1 mm) from Anjingo river (bridge 57 km from Bealanana).
In dorsal view, body elliptical (BW 58% of BL), maximal body width attained at mid-body (SBW 50% of BL), widely rounded snout. In lateral view, body depressed (BW 153% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 74% of BL), narrowly rounded snout. Moderately large eyes (ED 14% of BL), not visible from ventral view, positioned very high (EH 84% of BH) dorsally and directed dorsolaterally, situated almost at mid-body (SE 48% of BL), moderately wide distance between eyes (IOD 55% of BW). Very large elliptical nares (ND 4% of BL), marked with a marginal rim, positioned very high (NH 92% of BH) dorsally and oriented dorsally, situated nearer to eye than to snout (RN 166% of NP) and above eye level (NH 109% of EH), moderately wide distance between nares (IND 51% of IOD), dark spot on the back of the nares present. Moderately long sinistral spiracle (SL 20% of BL), directed posteriorly, visible from dorsal and ventral view and obvious from lateral view; inner wall free from body and its aperture opens posteriorly, rounded opening, situated on the distal 1/5 of the body (SS 80% of BL), located low on the body (SH 35% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 53% of HAB). Short medial vent tube (VL 9% of BL), not attached to ventral fin. Small dorsolateral glands present. Very short tail (TAL 142% of BL), maximal tail height lower than body height (MTH 90% of BH), tail height at midtail lower than body height and as high as maximal tail height (THM 90% of BH and 100% of MTH), tail height at the beginning of the tail lower than body height (TH 72% of BH). Developed caudal musculature (TMW 51% of BW, TMH 72% of BH, TMH of 100% of TH and 80% of MTH, TMHM 55% of THM and MTH). Tail muscle reaches tail tip. Low fins (DF 61% of TMHM, VF 18% of MTHM), dorsal fin higher than ventral fin at midtail (DF 344% of VF). Dorsal fin originates on the proximal 1/4 of the tail musculature, progresses almost parallel with the upper margin of tail musculature up to 1/3 of the tail where it increases gradually up to midtail, then remains straight until decreasing just close to the tail tip. Ventral fin originates on the proximal 1/4 of the tail musculature, progresses almost parallel with the lower margin of tail musculature up to 1/3 of the tail where it increases gradually up to midtail, then remains straight until decreasing just close to the tail tip. Maximal tail height located at midtail (DMTH 50% of TAL), lateral tail vein perceptible on the proximal half of the tail musculature, myosepta recognizable all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 64% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Very wide enlarged oral disk (ODW 93% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Double row of marginal papillae interrupted by a narrow gap on the upper labium (DG 37% of ODW), gap on the lower labium absent; total number of marginal papillae is 377. Two hundred and thirty two submarginal papillae, continuous on lower labium and laterally and dorsolaterally on upper labium. Very short and small rounded papillae with rounded tip, longest marginal papillae measured 0.16 mm and 0,25 mm for submarginal papillae, papillae visible from dorsal view. LTRF 8(6-8)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Short A_1 row ($A_{1\ len}$ 35% of ODW). Density of keratodonts varies from 52/mm to 167/mm, $A_{1\ den}$ 122/mm (total 314). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Long keratodonts (0.20 mm), only keratonts on P_1 and P_2 distinguishable from one another. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Upper jaw sheath absent but its trace still evident; narrow jaw sheath (JW 33% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in life: Generally orangish with brown patches. Brown melanic pigment positioned in deep integumental layers, separated from a (possibly epidermal) transparent outer skin layer leaving a discernible transparent lateral area surrounding the body. Body dorsum very dark with some irregularly golden spots scattered on the skin A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. The dorsum of the tail muscle has some dark patches. Myosepta visible on the tail dorsum., Laterally, the dark patches on the jugal area and the flank are covered by golden patches. Abdominal region silvery leaving a noticeable transparent spiracle. Tail musculature yellowish to orangish, covered by sparse brown spots coalesced to form patches following mainly the lateral tail vein and the myosepta in the half proximal of the tail musculature; and irregularly scattered patches on the half distal. Fins transparent, vessel traces are conspicuous on fins, mainly on the dorsal one. Ventrally, oral disk yellowish, gular and branchial regions reddish, heart hidden by silvery tissue; venter silver, intestinal coils not visible.
Coloration in preservative: Generally dark brown. Dark brown spots positioned in deep integumental layers, separated from a (possibly epidermal) transparent outer skin layer, leaving out laterally a conspicuous transparent area surrounding the body. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. The dark domino-like structures between the vertebral area and the abdominal region are recognizable. The abdominal region is very dark. The transparent area around the snout is patched. The dorsum of the tail musclepresents a variegated pattern. Myosepta visible on the tail dorsum. Laterally, jugal area covered by dense dark brown spots; abdominal region very dark leaving out a transparent discernible spiracle, intestinal coils invisible. Tail musculature pale, covered by sparse brown spots coalesced to form remarkable patches following mainly the lateral tail vein and the myosepta in the half proximal of the tail musculature; and irregularly scattered patches on the half distal. Fins transparent, with vessel traces mainly on the dorsal one. Ventrally, oral disk yellowish, gular and branchial regions reddish, heart hidden by silvery tissue; venter silver, intestinal coils not visible.
Variation: One other voucher specimens (ZCMV 13110- ZSM 486/2010) assigned to this candidate species from the same locality reveal the identical oral disk configuration and external pigmentation of this species.

Boophis sambirano [Ca48 ZCMV 13109]

The following description refers to one tadpole in developmental stage 27 (Field number ZCMV 13109, ZSM 0485/2010, BL 12.7 mm, TL 24.7 mm) from Anjingo river (bridge 57 km from Bealanana).
In dorsal view, body ovoidal (BW 54% of BL), maximal body width attained at midbody (SBW 48% of BL), widely rounded snout. In lateral view, body depressed (BW 145% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 66% of BL), narrowly rounded snout. Moderately large eyes (ED 12% of BL), not visible from ventral view, positioned very high (EH 83% of BH) dorsally and directed laterally, situated almost at mid-body (SE 45% of BL), wide distance between eyes (IOD 67% of BW). Moderately large elliptical nares (ND 3% of BL), marked with a marginal rim, positioned very high (NH 90% of BH) dorsally and oriented dorsally, situated nearer to eye than to snout (RN 167% of NP) and above eye level (NH 108% of EH), moderately wide distance between nares (IND 44% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 14% of BL), directed posteriorly, visible from dorsal and ventral view and obvious from lateral view; inner wall free from body and its aperture opens posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 74% of BL), located low on the body (SH 36% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 63% of HAB). Short medial vent tube (VL 8% of BL), not attached to ventral fin. Small dorsolateral glands present. Very short tail (TAL 141% of BL), maximal tail height lower than body height (MTH 95% of BH), tail height at midtail lower than body height and as high as maximal tail height (THM 95% of BH and 100% of MTH), tail height at the beginning of the tail lower than body height (TH 76% of BH). Developed caudal musculature (TMW 50% of BW, TMH 76% of BH, TMH of 100% of TH and 76% of MTH, TMHM 53% of THM and MTH). Tail muscle reaches tail tip. Low fins (DF 60% of TMHM, VF 30% of MTHM), dorsal fin higher than ventral fin at midtail (DF 201% of VF). Dorsal fin originates on the proximal 1/10 of the tail musculature, progresses almost parallel with the upper margin of tail musculature up to 1/3 of the tail where it increases gradually up to midtail, then remains almost parallel with dorsal margin of the tail musculature until decreasing just close to the tail tip. Ventral fin originates on the proximal 1/10 of the tail musculature, progresses almost parallel with the lower margin of tail musculature up to 1/3 of the tail where it increases gradually up to midtail, then remains almost parallel with the margin of the tail musculature until decreasing just close to the tail tip. Maximal tail height located at midtail (DMTH 50% of TAL), lateral tail vein perceptible on the proximal half of the tail musculature, myosepta recognizable all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 60% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Hyper-wide enlarged oral disk (ODW 108% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Double row of marginal papillae interrupted by a narrow gap on the upper labium (DG 37% of ODW), gap on the lower labium absent; total number of marginal papillae is 336. Two hundred and seventy two submarginal papillae, continuous on lower labium and laterally and dorsolaterally on upper labium. Very short and small rounded papillae with rounded tip, longest marginal papillae measured 0.11 mm and 0,18 mm for submarginal papillae, papillae visible from dorsal view. LTRF 8(6-8)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Short A_1 row ($A_{1\ len}$ 36% of ODW). Density of keratodonts varies from 51/mm to 148/mm, $A_{1\ den}$ 125/mm (total 330). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.15 mm), only keratonts on P_1 and P_2 distinguishable from one another. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Upper jaw sheath absent but its trace still evident; narrow jaw sheath (JW 31% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in life: Generally orangish with brown patches. Brown melanic pigment positioned in deep integumental layers, separated from a (possibly epidermal) transparent outer skin layer leaving a discernible transparent lateral area surrounding the body. Body dorsum very dark with some irregularly golden spots scattered on the skin A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. The dorsum of the tail muscle has some spots. Irregularly golden spots scattered on the skin, mainly on the body. Myosepta visible on the tail dorsum. Laterally, the dark patches on the jugal area and the flank are covered by golden patches. Abdominal region silvery leaving a noticeable transparent spiracle. Tail musculature yellowish to orangish andin the half proximal and almost free from pigents on the half distal; covered by sporadic brown spots surronding mainly the lateral tail vein and the myosepta in the half proximal of the tail musculature, and the dorsal and ventral edge of the tail muscle on the half distal. Fins transparent, vessel traces are conspicuous on fins, mainly on the dorsal one. Ventrally, oral disk yellowish, gular and branchial regions reddish, heart not hidden by silvery tissue; venter silver with black patches close to the branchial region and the vent tube, intestinal coils not visible.
Coloration in preservative: Generally dark brown. Dark brown spots positioned in deep integumental layers, separated from a (possibly epidermal) transparent outer skin layer, leaving out laterally a conspicuous transparent area surrounding the body. Body are covered by brown blotches which gives a more or less variegated pattern of the tadpole. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. The dark domino-like structures between the vertebral area and the abdominal region are recognizable. The abdominal region is very dark. The transparent area around the snout is patched. The dorsum of the tail musclepresents a variegated pattern. Myosepta visible on the tail dorsum. Laterally, jugal area covered by dense dark brown spots; abdominal region very dark leaving out a transparent discernible spiracle, intestinal coils invisible. Tail musculature pale, covered by brown spots coalesced to form patches surronding some myosepta in the half proximal of the tail musculature; and irregularly scattered sopts on the half distal. Fins transparent, with vessel traces mainly on the dorsal one. Ventrally, oral disk yellowish, gular and branchial regions reddish, heart hidden by silvery tissue; venter silver, intestinal coils not visible.
Variation: One other voucher specimens (ZCMV 13106- ZSM 483/2010) assigned to this candidate species from the same locality reveal the identical oral disk configuration and external pigmentation of this species. Living pictures of two additional voucher specimens (ZCMV 13107- ZSM 484/2010, ZCMV 13108- ZSM 485/2010) assigned to this species from the same locality show variation on the density and the tone of the pigmentation.

Boophis sambirano [Ca49 ZCMV 13155]

The following description refers to one tadpole in developmental stage 27 (Field number ZCMV 13155, ZSM 0528/2010, BL 11.7 mm, TL 26.7 mm) from Ankijagna Lagnana.
In dorsal view, body ovoidal (BW 66% of BL), maximal body width attained between the proximal 3/5 and 4/5 of the body (SBW 70% of BL), widely rounded snout. In lateral view, body depressed (BW 128% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 72% of BL), narrowly rounded snout. Moderately large eyes (ED 14% of BL), not visible from ventral view, positioned high (EH 72% of BH) dorsally and directed dorsolaterally, the proximal 1/5 and 2/5 of the body (SE 38% of BL), moderately wide distance between eyes (IOD 55% of BW). Very large elliptical nares (ND 5% of BL), marked with a marginal rim, positioned high (NH 70% of BH) dorsally and oriented dorsally, situated nearer to eye than to snout (RN 107% of NP) and at eye level (NH 98% of EH), moderately wide distance between nares (IND 46% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 16% of BL), directed posteriorly, visible from dorsal and ventral view and obvious from lateral view; inner wall free from body and its aperture opens posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 77% of BL), located low on the body (SH 28% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 45% of HAB). Moderately long medial vent tube (VL 11% of BL), not attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 163% of BL), maximal tail height lower than body height (MTH 90% of BH), tail height at midtail lower than body height and as high as maximal tail height (THM 90% of BH and 100% of MTH), tail height at the beginning of the tail lower than body height (TH 60% of BH). Developed caudal musculature (TMW 46% of BW, TMH 60% of BH, TMH 100% of TH and 72% of MTH, TMHM 54% of THM and MTH). Tail muscle reaches tail tip. Low fins (DF 56% of TMHM, VF 29% of MTHM), dorsal fin higher than ventral fin at midtail (DF 191% of VF). Dorsal fin originates on the proximal 1/10 of the tail musculature, progresses almost parallel with the upper margin of tail musculature up to 1/5 of the tail where it increases gradually up to its maximal height at mid-tail, then decreases gradually close to the tail tip. Ventral fin originates on the ventral terminus of the body, increases meticulously up to midtail, then remains straight until decreasing just close to the tail tip. Maximal tail height located at midtail (DMTH 50% of TAL), lateral tail vein perceptible on the proximal half of the tail musculature, myosepta recognizable all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 62% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Wide enlarged oral disk (ODW 95% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Double row of marginal papillae interrupted by a narrow gap on the upper labium (DG 23% of ODW), gap on the lower labium absent; total number of marginal papillae is 276. Two hundred and thirty eight submarginal papillae, continuous on lower labium and laterally and dorsolaterally on upper labium. Very short and small rounded papillae with rounded tip, longest marginal papillae measured 0.13 mm and 0,15 mm for submarginal papillae, papillae not visible from dorsal view. LTRF 8(6-8)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Short A_1 row ($A_{1\ len}$ 22% of ODW). Density of keratodonts varies from 56/mm to 181/mm, $A_{1\ den}$ 129/mm (total 163). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.14 mm), only keratonts on P_1 and P_2 distinguishable from one another. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Upper jaw sheath absent but its trace still evident; narrow jaw sheath (JW 33% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in life: Uniformly yelowish dark brown. Brown melanic pigment positioned in deeper dermal layers covered by golden pigments on the body. The transparent lateral area surrounding the body is indiscernible. The hexagonal mark above the neocranium is not obvious; the dark semicircular patch behind each narial opening is recognizeable. The dorsum of the tail muscle has some dark patches. Myosepta visible on the tail dorsum. Laterally, the dark patches on the jugal area and the flank are faded with golden patches. Abdominal region silvery leaving a noticeable transparent spiracle. Tail musculature yellowish covered by brown spots which condensed sometimes to form patches covering the whole tail musclulature. Fins transparent, vessel traces are conspicuous on fins, mainly on the dorsal one. Ventrally, oral disk yellowish, gular and branchial regions reddish, heart not hidden by silvery tissue; venter silver with black patches close to the branchial region and the vent tube, intestinal coils not visible.
Coloration in preservative: Predominantly pale-brownish. Dark brown spots positioned in deep integumental layers covered uniformly the dorsum and condensed to form dark patches especially between the eyes, behind the narial opening. Some few dermal brown patches scaterred sporadically on the body and tail dorsum. The dark domino-like structures between the vertebral area and the abdominal region are recognizable. The abdominal region is very dark. The snout is patched. The dorsum of the tail muscle presents some clear patches. Myosepta visible on the tail dorsum. Laterally, jugal area and surrounding the snout covered by dense dark brown spots positioned in deep integumental layers. abdominal region very dark leaving out a spoted discernible spiracle, intestinal coils not visible. Tail musculature pale,covered by dense reticulations, whose density dimishes toward the tail tip. Fins opaque, with scarced blotches on the dorsal fin and on the ventral fin close to the tail tip. Ventrally, oral disk, gular and branchial regions beige; venter dark, intestinal coils not visible.
Variation: Two other voucher specimens (ZCMV 13150- ZSM 523/2010 and ZCMV 13156- ZSM 529/2010) assigned to this candidate species from the same locality and many non-voucher specimen of the series reveal an identical oral disk configuration and external pigmentation of this species. Living pictures of six additional voucher specimens (ZCMV 13148- ZSM 521/2010, ZCMV 13149- ZSM 522/2010, ZCMV 13150- ZSM 523/2010, ZCMV 13152- ZSM 525/2010, ZCMV 13153- ZSM 526/2010, ZCMV 13154- ZSM 527/2010) assigned to this candidate species from the same locality show variation on the density and the tone of the pigmentation.

Boophis sambirano [Ca50 ZCMV 13172]

The following description refers to one tadpole in developmental stage 27 (Field number ZCMV 13172, ZSM 0545/2010, BL 11,7 mm, TL 25,7 mm) from Ambinanitelo.
In dorsal view, body elliptical (BW 60% of BL), maximal body width attained between the proximal 3/5 and 4/5 of the body (SBW 66% of BL), widely rounded snout. In lateral view, body depressed (BW 128% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 73% of BL), narrowly rounded snout. Moderately large eyes (ED 13% of BL), not visible from ventral view, positioned very high (EH 80% of BH) dorsally and directed dorsolaterally, situated almost at mid-body (SE 46% of BL), moderately wide distance between eyes (IOD 59% of BW). Very large elliptical nares (ND 4% of BL), marked with a marginal rim, positioned very high (NH 82% of BH) dorsally and oriented dorsally, situated in mid-distance between the eye and the snout (RN 103% of NP) and at eye level (NH 103% of EH), moderately wide distance between nares (IND 58% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 14% of BL), directed posteriorly, visible from dorsal and ventral view and obvious from lateral view; inner wall free from body and its aperture opens posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 79% of BL), located low on the body (SH 36% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 65% of HAB). Short medial vent tube (VL 8% of BL), not attached to ventral fin. Small dorsolateral glands present. Very short tail (TAL 142% of BL), maximal tail height lower than body height (MTH 91% of BH), tail height at midtail lower than body height and as high as maximal tail height (THM 91% of BH and 100% of MTH), tail height at the beginning of the tail lower than body height (TH 66% of BH). Developed caudal musculature (TMW 51% of BW, TMH 66% of BH, TMH of 100% of TH and 72% of MTH, TMHM 51% of THM and MTH). Tail muscle reaches tail tip. Low fins (DF 65% of TMHM, VF 33% of MTHM), dorsal fin higher than ventral fin at midtail (DF 198% of VF). Dorsal fin originates on the proximal 1/10 of the tail musculature, progresses almost parallel with the upper margin of tail musculature up to 1/5 of the tail where it increases gradually up to its maximal height at the 2/3 of the tail, then decreases gradually close to the tail tip. Ventral fin originates on the proximal 1/10 of the tail musculature, progresses almost parallel with the lower margin of tail musculature up to 1/3 of the tail where it increases gradually up to midtail, then remains straight until decreasing just close to the tail tip. Maximal tail height located at midtail (DMTH 50% of TAL), lateral tail vein perceptible on the proximal half of the tail musculature, myosepta recognizable all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 55% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Very wide enlarged oral disk (ODW 95% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Double row of marginal papillae interrupted by a narrow gap on the upper labium (DG 29% of ODW), gap on the lower labium absent; total number of marginal papillae is 323. Two hundred and fourty five submarginal papillae, continuous on lower labium and laterally and dorsolaterally on upper labium. Very short and small rounded papillae with rounded tip, longest marginal papillae measured 0.10 mm and 0,12 mm for submarginal papillae, papillae not visible from dorsal view. LTRF 8(6-8)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Short A_1 row ($A_{1\,len}$ 28% of ODW). Density of keratodonts varies from 66/mm to 159/mm, $A_{1\,den}$ 111/mm (total 280). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.14 mm), only keratonts on P_1 and P_2 distinguishable from one another. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Upper jaw sheath absent but its trace still evident; narrow jaw sheath (JW 32% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in life: Generally yelowish with brown patches. Brown pigment positioned in deeper dermal layers, separated from a (possibly epidermal) transparent outer skin layer, covering the dorsum and flank of the body. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. The dorsum of the tail muscle has some dark patches. Myosepta visible on the tail dorsum. Irregularly golden spots scattered on the skin, mainly on the body. Laterally, the dark patches on the jugal area and the flank are faded with the golden patches. Abdominal region silvery leaving a noticeable transparent spiracle. Tail musculature yellowish and in the half proximal and almost transparent on the half distal; covered by sparse brown spots following mainly the lateral tail vein and the myosepta in the half proximal of the tail musculature, and the dorsal and ventral edge of the tail muscle on the half distal. Fins transparent, vessel traces are conspicuous on fins, mainly on the dorsal one. Ventrally, oral disk yellowish, gular and branchial regions reddish, heart not hidden by silvery tissue; venter silver with black patches close to the branchial region and the vent tube, intestinal coils not visible.
Variation: Three other voucher specimens (ZCMV 13171- ZSM 544/2010, ZCMV 13173- ZSM 546/2010, ZCMV 13174- ZSM 547/2010) assigned to this candidate species from the same locality reveal an identical oral disk configuration and external pigmentation compared to the described voucher specimen.

Boophis marojezensis Glaw & Vences 1994

The following description refers to one tadpole in developmental stage 27 (Field number FGZC 2277, ZSM 1528/2007, BL 7.1 mm, TL 18.3 mm), from Marojejy Special Reserve.
In dorsal view, body elliptical (BW 58% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 55% of BL), widely rounded snout. In lateral view, body depressed (BW 117% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 67% of BL), narrowly rounded snout. Moderately large eyes (ED 14% of BL), not visible from ventral view, positioned high (EH 79% of BH) dorsally and directed dorsolaterally, situated between the proximal 4/10 and 5/10 of the body (SE 43% of BL), wide distance between eyes (IOD 67% of BW). Large rounded nares (ND 3% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 74% of BH) dorsally and oriented anterolaterally, situated nearer to eyes than to snout (RN 109% of NP) and at eye level (NH 94% of EH), moderately wide distance between nares (IND 53% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 19% of

BL), directed posterodorsally, visible from dorsal and ventral view and perceptible from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 74% of BL), located moderately high on the body (SH 53% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 84% of HAB). Short dextral vent tube (VL 8% of BL), inner wall absent, attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 181% of BL), maximal tail height equal to body height (MTH 98% of BH), tail height at midtail lower than body height and almost equal to maximal tail height (THM 93% of BH and 95% of MTH), tail height at the beginning of the tail lower than body height (TH 80% of BH). Developed caudal musculature (TMW 52% of BW, TMH 65% of BH, TMH of 81% of TH and 66% of MTH, TMHM 49% of THM and 47% of MTH). Tail muscle reaches tail tip. Very low fins (DF 61% of TMHM, VF 42% of MTHM), dorsal fin higher than ventral fin at midtail (DF 144% of VF). Dorsal fin originates on the dorsal body-tail junction, increases gradually up to its maximal height before midtail, and then decreases progressively to the tail tip. Ventral fin originates on the dorsal body-tail junction, remains almost parallel with the dorsal margin of caudal musculature up to the proximal 3/10 where it increases meticulously up to its maximal height at midtail, and then continues straight before it decreases just close to the tail tip. Maximal tail height before midtail (DMTH 43% of TAL), lateral tail not visible, myosepta visible on the proximal half of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 63% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Very wide enlarged oral disk (ODW 87% of BW), positioned and directed ventrally, maximal width in the middle. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Oral disk rounded when open. Double row of marginal papillae, gap on upper labium and the lower labium absent; total number of marginal papillae is 260. Six hundred and six submarginal papillae, continuous on lower and upper labia. Moderately elongated marginal papillae with rounded tip, longest marginal and submarginal papillae measured 0.12 mm, papillae not visible from dorsal view. LTRF 7(5-7)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\ len}$ 53% of ODW). Density of keratodonts varies from 56/mm to 140/mm, $A_{1\ den}$ 92/mm (total 191). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.13 mm), distinguishable from one another, A_1, A_2 and P_3 have smaller keratodonts. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath, narrow (JW 27% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.

Coloration in preservative: Generally beige brownish. Light brown patches positioned in deeper dermal layers, separated from a (possibly epidermal) transparent outer skin layer, covering the dorsum and flank of the body extend between eyes and nares, and on the vertebral and abdominal areas, leaving out laterally a slightly transparent area. Dorsal sides of head and trunk covered by brown spots. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening is obvious. The dark domino-like structures between the vertebral area and the abdominal region is not obvious; abdominal region darker. The dorsum of the tail muscle rather clear. Myosepta visible on the tail dorsum. Laterally, upper part of the jugal area provided by brown spots; flank dorsolaterally identical to the dorsal pattern, abdominal region dark leaving an opaque noticeable spiracle. Tail musculature spotted, mainly on the proximal 2/3, the distal 1/3 is rather clear. Light brown spots positioned in deeper dermal layers condensed to form patches sometimes reticulation mainly on the upper half of the tail musculature. Dark brown epidermal spots scattered irregularly. Fins transparent, upper fin speckled on the 1/4 and spotted until the 2/3, the distal 1/3 is free from pigment; ventral fin free from pigment. Ventrally, oral disk, gular and branchial regions pale; venter dark, intestinal coils not visible.

Variation: One other voucher specimens (FGZC 2953- ZSM 1628/2007) assigned to this species from the same locality reveal an identical oral disk configuration and external pigmentation compared to the described voucher specimen.

Boophis marojezensis [Ca25 Vieites et al. 2009]

The following description refers to one tadpole in developmental stage 29 (Field number FGZC 2929, ZSM 1611/2007, BL 7.8 mm, TL 18.5 mm), from Marojejy Special Reserve.

In dorsal view, body elliptical (BW 61% of BL), maximal body width attained between the proximal 3/5 and 4/5 of the body (SBW 70% of BL), narrowly rounded snout. In lateral view, body depressed (BW 117% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 70% of BL), widely rounded snout. Large eyes (ED 15% of BL), not visible from ventral view, positioned high (EH 74% of BH) dorsally and directed dorsolaterally, situated between the proximal 4/10 and 5/10 of the body (SE 41% of BL), wide distance between eyes (IOD 68% of BW). Large rounded nares (ND 4% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 71% of BH) dorsally and oriented anterolaterally, situated almost in mid-distance between the eye and the snout (RN 96% of NP) and at eye level (NH 97% of EH), moderately wide distance between nares (IND 53% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 19% of BL), directed posterodorsally, visible from dorsal and ventral view and perceptible from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 75% of BL), located low on the body (SH 34% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 57% of HAB). Very long dextral vent tube (VL 24% of BL), inner wall absent, attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 178% of BL), maximal tail height lower than body height (MTH 94% of BH), tail height at midtail lower than body height and as high as maximal tail height (THM 94% of BH and 100% of MTH), tail height at the beginning of the tail lower than body height (TH 87% of BH). Developed caudal musculature (TMW 57% of BW, TMH 62% of BH, TMH of 72% of TH and 66% of MTH, TMHM 55% of THM and 55% of MTH). Tail muscle reaches tail tip. Very low fins (DF 52% of TMHM, VF 32% of MTHM), dorsal fin higher than ventral fin at midtail (DF 163% of VF). Dorsal fin originates on the dorsal body-tail junction, remains almost parallel with the dorsal margin of caudal musculature up to the proximal 3/10 where it increases regularly up to its maximal height at midtail, and then continues straight before it decreases just close to the tail tip. Ventral fin originates on the dorsal body-tail junction, remains

almost parallel with the dorsal margin of caudal musculature up to the proximal 3/10 where it increases meticulously up to its maximal height at midtail, and then continues straight before it decreases just close to the tail tip. Maximal tail height almost at midtail (DMTH 47% of TAL), lateral tail vein perceptible all along the tail, myosepta visible on the proximal half of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 59% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Wide enlarged oral disk (ODW 68% of BW), positioned and directed ventrally, maximal width in the middle. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Oral disk rounded when open. Single row of marginal papillae, gap on upper labium and the lower labium absent; total number of marginal papillae is 222. Three hundred and fifteen submarginal papillae, continuous on lower and upper labia. Moderately elongated marginal papillae with rounded tip, longest marginal papillae measured 0.10 mm, and 0.05 mm for the submarginal ones, papillae not visible from dorsal view. LTRF 7(5-7)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\,len}$ 52% of ODW). Density of keratodonts varies from 48/mm to 80/mm, $A_{1\,den}$ 107/mm (total 126). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Short keratodonts (0.08 mm), distinguishable from one another, A_1, A_2 and P_3 have smaller keratodonts. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath absent; narrow jaw sheath (JW 30% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in preservative: Generally pale brownish. Light brown specks positioned in deeper dermal layers, separated from a (possibly epidermal) transparent outer skin layer, covering the dorsum and flank of the body extend between eyes and nares, and on the vertebral and abdominal areas, leaving out laterally a slightly transparent area. Dorsal sides of head and trunk covered by brown spots. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening is obvious. The dark domino-like structures between the vertebral area and the abdominal region is noticeable; abdominal region darker. The dorsum of the tail muscle spotted, and provided by few brown patches; density of spots diminishes toward tail tip. Myosepta visible on the tail dorsum. Laterally, jugal area provided by brown spots; flank dorsolaterally identical to the dorsal pattern, abdominal region spotted leaving an opaque discernible spiracle above the intestinal coils. Tail musculature spotted, mainly on the proximal half. Some spots condensed to form more or less rounded distinct patches. Fins transparent, almost free from pigments. Ventrally, oral disk, gular and branchial regions pale; venter dark, intestinal coils not visible.
Variation: The presence of condensed spots to form more or less rounded distinct patches on the tail musculature is found on two non voucher specimens of the same series.

Boophis marojezensis [Ca26 Vieites et al. 2009]

The following description refers to one tadpole in developmental stage 29 (Field number FGZC 2930, ZSM 1612/2007, BL 8.8 mm, TL 20.6 mm), from Marojejy Special Reserve.
In dorsal view, body elliptical (BW 56% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 55% of BL), narrowly rounded snout. In lateral view, body depressed (BW 110% of BH), maximal body height attained between the proximal 2/5 and 3/5 of the body (SBH 58% of BL), widely rounded snout. Large eyes (ED 15% of BL), not visible from ventral view, positioned high (EH 68% of BH) dorsally and directed dorsolaterally, situated between the proximal 4/10 and 5/10 of the body (SE 40% of BL), wide distance between eyes (IOD 73% of BW). Large rounded nares (ND 3% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 63% of BH) dorsally and oriented anterolaterally, situated closer to snout than to eye (RN 85% of NP) and below eye level (NH 92% of EH), moderately wide distance between nares (IND 49% of IOD), dark spot on the back of the nares present. Sort sinistral spiracle (SL 17% of BL), directed posterodorsally, visible from dorsal and ventral view and perceptible from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 75% of BL), located low on the body (SH 34% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 54% of HAB). Moderately long dextral vent tube (VL 12% of BL), inner wall absent, attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 178% of BL), maximal tail height lower than body height (MTH 96% of BH), tail height at midtail almost equal to body height and as high as maximal tail height (THM 96% of BH and 100% of MTH), tail height at the beginning of the tail lower than body height (TH 85% of BH). Developed caudal musculature (TMW 57% of BW, TMH 63% of BH, TMH of 74% of TH and 65% of MTH, TMHM 52% of THM and 52% of MTH). Tail muscle reaches tail tip. Very low fins (DF 57% of TMHM, VF 36% of MTHM), dorsal fin higher than ventral fin at midtail (DF 159% of VF). Dorsal fin originates on the dorsal body-tail junction, remains almost parallel with the dorsal margin of caudal musculature up to the proximal 3/10 where it increases regularly up to its maximal height at midtail, and then continues straight before it decreases just close to the tail tip. Ventral fin originates on the dorsal body-tail junction, remains almost parallel with the dorsal margin of caudal musculature up to the proximal 3/10 where it increases meticulously up to its maximal height at midtail, and then continues straight before it decreases just close to the tail tip. Maximal tail height almost at midtail (DMTH 49% of TAL), lateral tail vein perceptible all along the tail, myosepta visible on the proximal half of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 62% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Wide enlarged oral disk (ODW 74% of BW), positioned and directed ventrally, maximal width in the middle. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Oral disk rounded when open. Single row of marginal papillae, gap on upper labium and the lower labium absent; total number of marginal papillae is 234. Four hundred and thirty submarginal papillae, continuous on lower and upper labia. Moderately long elongated marginal papillae with rounded tip, longest marginal papillae measured 0.17 mm, and 0.08 mm for the submarginal ones, papillae not visible from dorsal view. LTRF 7(5-7)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\,len}$ 51% of ODW). Density of keratodonts varies from 35/mm to 94/mm, $A_{1\,den}$ 84/mm (total 155). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.13 mm), distinguishable from one another, A_1, A_2

and P_3 have smaller keratodonts. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath, narrow (JW 32% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in preservative: Generally pale brownish. Light brown specks positioned in deeper dermal layers, separated from a (possibly epidermal) transparent outer skin layer, extend between eyes and nares, and on the vertebral and abdominal areas, leaving out laterally a slightly transparent area. Dorsal sides of head and trunk provided by brown spots which coalesce in some area to form patches or reticulations. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening is obvious. The dark domino-like structures between the vertebral area and the abdominal region is noticeable; abdominal region darker. The dorsum of the tail muscle is speckled and spotted, and provided by few brown patches; density of spots and specks diminishes towards tail tip. Myosepta visible on the tail dorsum. Laterally, jugal area provided by brown spots; flank dorsolaterally identical to the dorsal pattern, abdominal region spotted leaving an opaque discernible spiracle above the intestinal coils. Tail musculature spotted, mainly on the proximal half. Density of spots diminishes towards tail tip. Ventrally, oral disk, gular and branchial regions pale; venter dark, intestinal coils not visible.

Boophis marojezensis [Ca51 ZCMV 3691]

The following description refers to one tadpole in developmental stage 25 (Field number ZCMV 3691, ZSM 267/2008, BL 6 mm, TL 20 mm) from Ranomafana National Park.
In dorsal view, body elliptical (BW 55% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 51% of BL), narrowly rounded snout. In lateral view, body depressed (BW 106% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 68% of BL), widely rounded snout. Large eyes (ED 18% of BL), not visible from ventral view, positioned very high (EH 80% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 35% of BL), very wide distance between eyes (IOD 86% of BW). Large rounded nares (ND 3% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 72% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 78% of NP) and below eye level (NH 90% of EH), moderately wide distance between nares (IND 45% of IOD), dark spot on the back of the nares present. Moderately long sinistral spiracle (SL 20% of BL), directed posterodorsally, visible from ventral view and perceptible from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 65% of BL), located low on the body (SH 37% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 60% of HAB). Moderately long dextral vent tube (VL 10% of BL), inner wall absent, attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 167% of BL), maximal tail height lower than body height (MTH 85% of BH), tail height at midtail lower than body height (THM 82% of BH) and almost equal to maximal tail height (THM 96% of MTH), tail height at the beginning of the tail lower than body height (TH 80% of BH). Developed caudal musculature (TMW 68% of BW, TMH 69% of BH, TMH of 86% of TH and 81% of MTH, TMHM 69% of THM and 66% of MTH). Tail muscle reaches tail tip. Very low fins (DF 30% of TMHM, VF 15% of MTHM), dorsal fin higher than ventral fin at midtail (DF 193% of VF). Dorsal fin originates at the proximal 2/5 of the tail, increases abruptly up to its maximal height at midtail, and then continues straight before it decreases just close to the tail tip. Ventral fin originates at the proximal 2/5 of the tail, increases gradually up to its maximal height at mid tail, and remains almost parallel with the lower margin before it decreases close to the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 57% of TAL), lateral tail vein visible all along the tail, myosepta perceptible all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 62% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Wide enlarged oral disk (ODW 72% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Oral disk rounded when open. Single row of marginal papillae, gap on upper and lower labium absent; total number of marginal papillae is 279. Three hundred and nine submarginal papillae, continuous on lower and upper labia. Short and small conical marginal papillae with rounded tip, longest marginal papillae and submarginal measured 0.10 mm, papillae not visible from dorsal view. LTRF 7(5-7)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\,len}$ 49% of ODW). Density of keratodonts varies from 35/mm to 106/mm, $A_{1\,den}$ 83/mm (total 146). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.10 mm), distinguishable from one another, A_1, A_2 and P_3 have smaller keratodonts. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath, narrow (JW 35% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in life: Generally yellow brownish. Dorsally, body covered by brown spots. A dark semicircular patch behind each narial opening extends below the eyes and an hexagonal mark above the neocranium is present. The dark domino-like structures between the vertebral area and the abdominal region are recognizable, but overlain by golden patches. The proximal quarter of the dorsal part of the tail muscle free from pigments. Some blotches of silver pigments scattered on the tail muscle. Myosepta visible on the tail dorsum. Laterally, jugal area covered by dense dark brown spots; flank dorsolaterally identical to the dorsal pattern, ventrolaterally silvery; abdominal region very dark and overlain by golden patches leaving a noticeable transparent spiracle. Tail musculature yellowish, provided by dense spots which group in some areas to form dark patches. Fins transparent, dorsal fin blotched, ventral fin free from pigments. Ventrally, oral disk yellowish, gular and branchial regions reddish, heart hidden by golden tissue; venter golden, intestinal coils not visible.
Coloration in preservative: Tadpole concords with the upper description except that it is paler. The silver tissue which hides the heart and silver venter becomes whitish. The red banchial area becomes pale.
Variation: Twenty one other voucher specimens (T 394- ZSM 1008/2007, T 432- ZSM 117/2007, T 09/1088-779/2008, T 09/1091-780/2008, T 09/1094-781/2008, ZCMV 3629- ZSM 318/2008, ZCMV 3635- ZSM 232/2008, ZCMV 3690- ZSM 266/2008, ZCMV 3742- ZSM 481/2008, ZCMV 4203- ZSM 401/2007, ZCMV 4264- ZSM 457/2007, ZCMV 4376- ZSM

1453/2007, ZCMV 4531- ZSM 532/2007, ZCMV 4541- ZSM 504/2007, ZCMV 4547- ZSM 1390/2007, ZCMV 4550- ZSM 509/2007, ZCMV 4931- ZSM 838/2007, ZCMV 5098- ZSM 913/2007, ZCMV 5986- ZSM 1212/2007, ZCMV 1395- ZSM 0025/2007, T 09/1085-778/2008) assigned to this candidate species from the same locality reveal an identical oral disk configuration and external pigmentation compared to the described voucher specimen.

Boophis marojezensis [Ca52 ZCMV 13168]

The following description refers to one tadpole in developmental stage 28 (Field number ZCMV 13168, ZSM 541/2010, BL 10.5 mm, TL 26.1 mm) from Ambinanitelo.
In dorsal view, body elliptical (BW 59% of BL), maximal body width attained between the proximal 3/5 and 4/5 of the body (SBW 65% of BL), narrowly rounded snout. In lateral view, body depressed (BW 119% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 71% of BL), widely rounded snout. Large eyes (ED 16% of BL), not visible from ventral view, positioned high (EH 73% of BH) dorsally and directed dorsolaterally, situated between the proximal 4/10 and 5/10 of the body (SE 41% of BL), wide distance between eyes (IOD 72% of BW). Large rounded nares (ND 3% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 70% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 92% of NP) and almost at eye level (NH 95% of EH), moderately wide distance between nares (IND 47% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 17% of BL), directed posterodorsally, visible from dorsal and ventral views and perceptible from lateral view; inner wall free from body and its aperture opens posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 72% of BL), located low on the body (SH 35% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 62% of HAB). Moderately long dextral vent tube (VL 10% of BL), inner wall absent, attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 189% of BL), maximal tail height lower than body height (MTH 71% of BH), tail height at midtail as high as body height (THM 102% of BH) and maximal tail height (THM 98% of MTH), tail height at the beginning of the tail lower than body height (TH 81% of BH). Developed caudal musculature (TMW 59% of BW, TMH 71% of BH, TMH of 88% of TH and 68% of MTH, TMHM 52% of THM and 51% of MTH). Tail muscle reaches tail tip. Very low fins (DF 56% of TMHM, VF 36% of MTHM), dorsal fin higher than ventral fin at midtail (DF 155% of VF). Dorsal fin originates on the dorsal body-tail junction, increases regularly up to its maximal height at midtail, and then continues straight until the ¾ of the tail where it decreases just close to the tail tip. Ventral fin originates at the ventral terminus of the body, increases gradually up to its maximal height at mid tail, and remains almost parallel with the lower margin before it decreases close to the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 45% of TAL), lateral tail vein and myosepta perceptible on the half proximal of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 56% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Wide enlarged oral disk (ODW 62% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Oral disk rounded when open. Single row of marginal papillae, gap on upper and lower labium absent; total number of marginal papillae is 258. Five hundred end twenty two submarginal papillae, continuous on lower and upper labia. Short and small conical marginal papillae with rounded tip, longest marginal papillae measured 0,07 mm and 0,08 for submarginal, papillae not visible from dorsal view. LTRF 7(5-7)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\,len}$ 50% of ODW). Density of keratodonts varies from 53/mm to 92/mm, $A_{1\,den}$ 81/mm (total 156). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.16 mm), distinguishable from one another, A_1, A_2 and P_3 have smaller keratodonts. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath, narrow (JW 32% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in life: Generally brown reddish. Light brown specks positioned in deeper dermal layers, separated from a (possibly epidermal) transparent outer skin layer. A dark semicircular patch behind each narial opening and a hexagonal mark above the neocranium is present. Reddish gills are seen through from dorsal view. Some golden spots scattered on the skin. The dorsum of the tail muscle is speckled and spotted, and provided by few brown patches; density of spots and specks diminishes towards tail tip. Myosepta visible on the tail dorsum. Laterally, jugal area covered by sparse light brown and golden spots; flank dorsolaterally identical to the dorsal pattern, ventrolaterally silvery; reddish gills visible, spiracle not prceptible, abdominal region silver. Tail musculature reddish faded into transparent in the half distal, provided by light brown sparsed spots which density diminishes toward tail tip. Fins transparent, dorsal fin blotched, ventral fin free from pigments. Ventrally, oral disk yellowish, gular and branchial regions reddish, heart hidden by golden tissue; venter golden, intestinal coils not visible.
Coloration in preservative: Tadpole concords with the upper description except that it is paler. The red banchial area becomes pale.
Variation: One other voucher specimens (ZCMV 13169- ZSM 542/2010) assigned to this candidate species from the same locality reveal the identical oral disk configuration and external pigmentation of this species.

Boophis marojezensis [Ca53 ZCMV 13200]

The following description refers to one tadpole in developmental stage 27 (Field number ZCMV 13200, ZSM 573/2010, BL 9.6 mm, TL 23 mm) from Tsaratanana Integral Reserve.
In dorsal view, body elliptical (BW 60% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 56% of BL), narrowly rounded snout. In lateral view, body depressed (BW 138% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 71% of BL), widely rounded snout. Moderately large eyes (ED 14% of BL), not visible from ventral view, positioned high (EH 76% of BH) dorsally and directed dorsolaterally, situated at mid-body (SE 47% of BL), wide distance between eyes (IOD 67% of BW). Large rounded nares (ND 3% of BL), marked with a marginal

rim provided by a small dorsal projection, positioned high (NH 70% of BH) dorsally and oriented anterolaterally, situated almost in mid-distance between the eye and the snout (RN 96% of NP) and below eye level (NH 92% of EH), moderately wide distance between nares (IND 51% of IOD), dark spot on the back of the nares present. Short spiracle (SL 16% of BL), directed posterodorsally, visible from dorsal and ventral views and perceptible from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, rounded opening, situated in the distal 1/5 of the body (SS 81% of BL), located moderately high on the body (SH 44% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 73% of HAB). Moderately long dextral vent tube (VL 13% of BL), inner wall absent, attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 182% of BL), maximal tail height higher than body height (MTH 116% of BH), tail height at midtail higher than body height (THM 111% of BH) and lower than maximal tail height (THM 95% of MTH), tail height at the beginning of the tail lower than body height (TH 78% of BH). Developed caudal musculature (TMW 53% of BW, TMH 64% of BH, TMH of 82% of TH and 55% of MTH, TMHM 47% of THM and 47% of MTH). Tail muscle reaches tail tip. Very low fins (DF 72% of TMHM, VF 41% of MTHM), dorsal fin higher than ventral fin at midtail (DF 176% of VF). Dorsal fin originates on the dorsal body-tail junction, increases regularly up to its maximal height at midtail, and then continues straight before it decreases just close to the tail tip. Ventral fin originates at the ventral terminus of the body, increases gradually up to its maximal height at mid tail, and remains almost parallel with the lower margin before it decreases close to the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 43% of TAL), lateral tail vein and myosepta perceptible on the half proximal of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 60% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Wide enlarged oral disk (ODW 68% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Oral disk rounded when open. Single row of marginal papillae, gap on upper and lower labium absent; total number of marginal papillae is 243. Four hundred and fifty two submarginal papillae, continuous on lower and upper labia. Short and small conical marginal papillae with rounded tip, longest marginal papillae measured 0,08 mm and 0.11 mm for submarginal papillae, papillae not visible from dorsal view. LTRF 7(5-7)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\,len}$ 44% of ODW). Density of keratodonts varies from 59/mm to 126/mm, $A_{1\,den}$ 126/mm (total 225). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Moderately long keratodonts (0.17 mm), distinguishable from one another, A_1, A_2 and P_3 have smaller keratodonts. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath, narrow (JW 35% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wider, completely keratinized and ribbed.

Coloration in life: Generally yellowish. Dark brown specks positioned in deeper dermal layers, separated from a (possibly epidermal) transparent outer skin layer recognizable. A dark semicircular patch behind each narial opening and a hexagonal mark above the neocranium is present. Some golden patches scattered on the body and the tail muscle. The dorsum of the tail muscle is speckled and spotted, density of spots and specks diminishes towards tail tip. Myosepta visible on the tail dorsum. Laterally, jugal area covered by sparse golden spots; flank dorsolaterally and abdominal region covered by golden patches, ventrolaterally silvery; spiracle not prceptible, abdominal region silver. Tail musculature yellowish provided by finely light brown sparsed spots which density diminishes toward tail tip. Fins transparent, dorsal fin speckled, ventral fin free from pigments. Ventrally, oral disk yellowish, gular and branchial regions reddish, heart hidden by golden tissue; venter golden, intestinal coils not visible.

Coloration in preservative: Tadpole concords with the upper description except that it is paler. The red banchial area becomes pale.

Variation: One other voucher specimens (ZCMV 13201- ZSM 574/2010) assigned to this candidate species from the same locality reveal the identical oral disk configuration and external pigmentation of this species. Living pictures of five other voucher specimens (ZCMV 13201- ZSM 574/2010, ZCMV 13202- ZSM 575/2010, ZCMV 13203- ZSM 576/2010, ZCMV 13204- ZSM 577/2010, ZCMV 13205- ZSM 578/2010) assigned to this candidate species from the same locality show variation on the density and the tone of the spots change.

Boophis vittatus Glaw, Vences, Andreone & Vallan 2001

The following description refers to one tadpole in developmental stage 29 (Field number FGZC 2238, ZSM 1906/2007, BL 7.8 mm, TL 18.5 mm), from R S Marojejy - Camp Mantella.

In dorsal view, body elliptical (BW 53% of BL), maximal body width attained at midbody (SBW 50% of BL), narrowly rounded snout. In lateral view, body depressed (BW 120% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 71% of BL), widely rounded snout. Large eyes (ED 15% of BL), not visible from ventral view, positioned high (EH 69% of BH) dorsally and directed dorsolaterally, situated between the proximal 4/10 and 5/10 of the body (SE 44% of BL), wide distance between eyes (IOD 69% of BW). Large rounded nares (ND 4% of BL), marked with a marginal rim provided by a small dorsal projection, positioned high (NH 70% of BH) dorsally and oriented anterolaterally, situated in mid-distance between the eye and the snout (RN 103% of NP) and at eye level (NH 101% of EH), moderately wide distance between nares (IND 46% of IOD), dark spot on the back of the nares present. Short sinistral spiracle (SL 16% of BL), directed posterodorsally, visible from ventral view and perceptible from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 76% of BL), located low on the body (SH 31% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 57% of HAB). Very short dextral vent tube (VL 4% of BL), inner wall absent, attached to ventral fin. Small dorsolateral glands present. Short tail (TAL 188% of BL), maximal tail height as high as body height (MTH 102% of BH), tail height at midtail as high as body height and maximal tail height (THM 101% of BH and 99% of MTH), tail height at the beginning of the tail lower than body height (TH 94% of BH). Developed caudal musculature (TMW 59% of BW, TMH 80% of BH, TMH of 86% of TH and 79% of MTH, TMHM 59% of THM and 58% of MTH). Tail muscle reaches tail tip. Very low

fins (DF 38% of TMHM, VF 32% of MTHM), dorsal fin higher than ventral fin at midtail (DF 118% of VF). Dorsal fin originates on the dorsal body-tail junction, remains almost parallel with the dorsal margin of caudal musculature up to the proximal ¼ where it increases regularly up to its maximal height at midtail, and then continues straight before it decreases just close to the tail tip. Ventral fin originates on the dorsal body-tail junction, remains almost parallel with the dorsal margin of caudal musculature up to the proximal ¼ where it increases meticulously up to its maximal height at midtail, and then continues straight before it decreases just close to the tail tip. Maximal tail height located between the proximal 1/5 and 2/5 of the tail (DMTH 39% of TAL), lateral tail vein perceptible all along the tail, myosepta visible on the proximal half of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 57% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip widely rounded. Wide enlarged oral disk (ODW 78% of BW), positioned and directed ventrally, maximal width in the centre. Oral disk not visible from dorsal view, anterior margin is separated by a deep crevice to the snout, i.e the entire margin is free from the snout. Oral disk rounded when open. Single row of marginal papillae, gap on upper labium and the lower labium absent; total number of marginal papillae is 289. Three hundred and twenty six submarginal papillae, continuous on lower and upper labia. Short and small conical marginal papillae with rounded tip, longest marginal papillae measured 0.09 mm, and 0.05 mm for the submarginal ones, papillae not visible from dorsal view. LTRF 7(5-7)/3 after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\ len}$ 50% of ODW). Density of keratodonts varies from 62/mm to 116/mm, $A_{1\ den}$ 107/mm (total 132). Gap in A_2 absent. Row alignment regular, P_1 uninterrupted. Short keratodonts (0.08 mm), distinguishable from one another, A_1, A_2 and P_3 have smaller keratodonts. Distal keratodonts much smaller than those in the middle; tight space between marginal papillae and keratodont rows. Totally keratinized upper jaw sheath absent; narrow jaw sheath (JW 38% of ODW). Lower jaw sheath U-shaped with widely rounded serrations, higher than wide, completely keratinized and ribbed.
Coloration in preservative: Generally pale brownish. Dorsal sides of head and trunk covered by brown spots which condense to form patches or reticulations. A hexagonal mark above the neocranium and a dark semicircular patch behind each narial opening are obvious. The dark domino-like structures between the vertebral area and the abdominal region are recognizable. The abdominal region is darker. The dorsum of the tail muscle reticulated, interrupted by light areas, density of reticulations diminishes towards tail tip. Myosepta visible on the tail dorsum. Laterally, jugal area provided by brown spots; flank dorsolaterally identical to the dorsal pattern, abdominal region very dark leaving a transparent discernible spiracle, intestinal coils invisible. Tail musculature pale, provided by brown spots which coalesce to form reticulations in the proximal part of the tail and become patches in the distal part. Fins transparent, with few brown spots on the dorsal fin, ventral fin free from pigment. Ventrally, oral disk, gular and branchial regions pale; venter dark, intestinal coils not visible.
Variation: Three other voucher specimens (FGZC 2237- ZSM 5219/2005, FGZC FGZC 2251- ZSM 1907/2007, FGZC 2914- ZSM 1601/2007) assigned to this species from the same locality reveal an identical oral disk configuration and external pigmentation.

Mantidactylus femoralis (Boulenger 1882)

The following description refers to one tadpole in developmental stage 28 (field number ZCMV 3431-ZSM 1736/2007, BL 11.4 mm, TL 34 mm) from the stream Andohan'i Sity (transect 1) in An'Ala forest. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of a *Mantidactylus femoralis* adult specimen (accession AY324812) from Andasibe.
In dorsal view, body elliptical (BW 57% of BL), maximal body width between the proximal 2/3 and 3/5 of the body (SBW 47% of BL), with a constriction behind the point of the maximal body width, narrowly rounded snout. In lateral view, body depressed (BW 141% of BH), maximal body height between the proximal 3/5 and 4/5 of the body (SBH 70% of BL), pointed snout. Moderately large eyes (ED 10% of BL), not visible from ventral view, positioned high (EH 73% of BH) dorsally and directed laterally, situated between the proximal 3/10 and 4/10 of the body (SE 32% of BL), moderately wide distance between eyes (IOD 52% of BW). Small elliptical nares (ND 1.1% of BL), marked with a marginal rim, positioned high (NH 60% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 83% of NP) and below eye level (NH 83% of EH), moderately wide distance between nares (IND 58% of IOD), red colored region on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 16% of BL), directed posteriorly, visible from dorsal and ventral views, perceivable from lateral view; inner wall free from body and its aperture opens posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 65% of BL), located high on the body (SH 69% of BH) and almost at the height of the point where the axis of the tail myotomes contacts the body (SH 96% of HAB). Moderately long dextral vent tube (VL 13% of BL), attached to ventral fin, inner wall present. No gland. Short tail (TAL 198% of BL), maximal tail height higher than body height (MTH 109% of BH), tail height at midtail almost equal to body height and lower than maximal tail height (THM 95% of BH and 87% of MTH), tail height at the beginning of the tail lower than body height (TH 85% of BH). Moderately developed caudal musculature (TMW 51% of BW, TMH 68% of BH, TMH of 80% of TH and 62% of MTH, TMHM 58% of THM and 50% of MTH). Tail muscle reaches tail tip. Very low fin type (DF 40% of TMHM, VF 37% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 107% of VF). Dorsal fin originates on tail muscle on the proximal 1/5 of the tail, increases abruptly to attain its maximal height before midtail and then progresses horizontally until the 9/10 of the tail and finally decreases gradually towards the tail tip. Ventral fin originates at the ventral terminus of the body, remains parallel with tail muscle almost to tail tip, then decreases to tail tip. Maximal tail height located between the proximal 1/5 and 2/5 of the tail (DMTH 40% of TAL), lateral tail vein and myosepta slightly visible on the proximal ¾ of the tail musculature, point where the

axis of the tail myotomes contacts the body in the upper half of the body height (HAB 72% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.
Small reduced oral disk (ODW 24% of BW), positioned ventrally and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 48% of ODW), gap on the lower labium absent; total number of marginal papillae 59. Sixty-nine submarginal papillae on the lower labium and laterally on upper labium. Short and moderately wide conical papillae with rounded tips, longest marginal papillae measured 0.15 mm and 0.16 mm for submarginal papillae, papillae visible from dorsal view. LTRF 3(2-3)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\,len}$ 45% of ODW). Density of keratodonts varies from 35/mm to 50/mm, $A_{1\,den}$ 39/mm (total 48). Wide gap in the first anterior interrupted row (A_{2gap} 66% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_2 and P_3 scattered. Short discernible keratodonts (0.06 mm). Distal keratodonts have the same lengths as those in the middle; prominent space between marginal papillae and keratodont rows. Partially keratinized upper jaw sheath, edge of the medial convexity black colored and the rest whitish; finely pointed serrations; moderately wide jaw sheath (JW 48% of ODW) with a short widely rounded medial convexity (MCL 18% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.
Coloration in preservative: Uniformly dark brown. Brown melanic pigment positioned in deeper dermal layers, separated from a (possibly epidermal) transparent outer skin layer, covering the dorsum and flank of the body. Some dark brown patches scattered on the dorsal skin. Laterally, jugal area (under eyes and nares) and flank covered by dark brown reticulations. The spiracle is reticulated at the base and transparent at the end, and detectable, and is situated the visible intestinal coils. Lower part of the flank not pigmented. Tail musculature overlain by dark brown reticulations. Fins pale, dorsal fin with sparse brown reticulations. Ventrally, oral disk, gular and branchial regions patched; venter pale, intestinal coils perceptible and regularly spiral shaped.
Variation: Six voucher specimen (ZSM 1554/2007-ZCMV 3536, ZSM 1555/2007-ZCMV 3537, ZSM 1733/2007-ZCMV 3428, ZSM 1781/2007-ZCMV 3476, ZSM 1834/2007-ZCMV 3554, ZSM 1848/2007-ZCMV 3572) from the same locality show a similar oral disk configuration.

Mantidactylus ambreensis Mocquard 1895

The following description refers to one tadpole in developmental stage 25 (field number FG/MV 2002.1950-ZSM 762/2004, BL 5.7 mm, TL 18.4 mm) from a stream crossing the the track 'Voie des milles arbres' at the Montagne d'Ambre National Park. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult specimen of *Mantidactylus ambreensis* (accession AY324822) from the same locality.
In dorsal view, body ovoid (BW 55% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 43% of BL), narrowly rounded snout. In lateral view, body depressed (BW 127% of BH), maximal body height attained at the 3/5 of the body (SBH 60% of BL), narrowly rounded snout. Moderately large eyes (ED 11% of BL), not visible from ventral view, positioned high (EH 68% of BH) dorsally and directed laterally, situated between the proximal 3/10 and 4/10 of the body (SE 37% of BL), wide distance between eyes (IOD 66% of BW). Moderately large rounded nares (ND 2.3% of BL), marked with a marginal rim, positioned moderately high (NH 58% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 67% of NP) and below eye level (NH 85% of EH), wide distance between nares (IND 65% of IOD), no dark spot on the back of the nares, ornamentation absent. Short sinistral spiracle (SL 14% of BL), directed posteriodorsally, visible from dorsal and ventral views, perceptible from lateral view; inner wall free from body and formed such that aperture opens laterally instead of posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 72% of BL), located moderately high on the body (SH 55% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 85% of HAB). Short dextral vent tube (VL 9% of BL), attached to ventral fin, inner wall present. No gland. Moderately long tail (TAL 225% of BL), maximal tail height lower than body height (MTH 94% of BH), tail height at midtail lower than body height and maximal tail height (THM 83% of BH and 87% of MTH), tail height at the beginning of the tail lower than body height (TH 85% of BH). Developed caudal musculature (TMW 55% of BW, TMH 74% of BH, TMH of 80% of TH and 79% of MTH, TMHM 62% of THM and 55% of MTH). Tail muscle reaches tail tip. Very low fin type (DF 33% of TMHM, VF 26% of MTHM), higher than ventral fin at mid-tail (DF 124% of VF). Dorsal fin originates between the dorsal body-tail junction and the proximal 1/4 of tail, ascends to attain its maximal height before midtail and then continues straight until the proximal ¾ of the tail, and then decreases towards the tail tip. Ventral fin originates at the ventral terminus of the body, remains straight until the proximal ¾ of the tail, and then decreases towards the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 45% of TAL), lateral tail vein not visible, myosepta perceptible on the proximal ½ of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 65% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.

Small reduced oral disk (ODW 35% of BW), positioned and directed ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a wide gap on the upper labium (DG 66% of ODW), gap on the lower labium absent; total number of marginal papillae is 30. Eighteen submarginal papillae, continuous on the lower labium and laterally on upper labium. Very short and small rounded papillae with rounded tips, longest marginal and submarginal papillae measured 0.08 mm, papillae not visible from dorsal view. LTRF 2(2)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Long A_1 row ($A_{1\ len}$ 65% of ODW). Density of keratodonts varies from 29/mm to 52/mm, $A_{1\ den}$ 29/mm (total 21). Moderately wide gap in the first anterior interrupted row (A_{2gap} 58% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_3 scattered. Very short distinguishable keratodonts (0.04 mm). Distal keratodont have same length as those in the middle; prominent space between marginal papillae and keratodont rows. Partially keratinized upper jaw sheath, edge of the medial convexity black colored and the rest whitish colored; finely pointed serrations; moderately wide jaw sheath (JW 53% of ODW) with a short widely pointed medial convexity (MCL 17% of JW). Lower jaw sheath V-shaped, partially keratinized and completely hidden by the upper jaw sheath.

Coloration in preservative: Generally beige-brownish. Dorsal sides of the head and trunk and higher part of the flank beige with light brown reticulations between nares and eyes, on the frontal, between the eyes, along the vertebral area and on the dorsolateral abdominal wall. Region between the vertebral area and the dorsolateral abdominal wall not pigmented except the area close to the body-tail junction. Laterally, jugal area and flank covered by sparse dark brown melanic reticulations leaving out a merged transparent spiracle above the well visible intestinal coils. Lower part of the flank not pigmented. Tail musculature beige with brown blotches of melanophores which fuse in some areas to form networks up to the tail tip. Fins translucent, dorsal fin with few patches. Ventrally, oral disk, gular and branchial regions pale; venter transparent, intestinal coils visible and regularly spiral shaped.

Variation: Four non-voucher specimens belonging to the same series show the same external morphology as the voucher specimen, in particular in the oral . However, LTRF varies between 2(2)/3(1-2) and 3(2-3)/3(1-2).

Mantidactylus zolitschka Glaw & Vences 2004

The following description refers to one tadpole in developmental stage 27 (field number ZCMV 3565-ZSM 1843/2007, BL 9.2 mm, TL 24.6 mm) from the stream Andohan'i Sity (transect 2) in An'Ala forest. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult specimen of *Mantidactylus zolitschka* (accession no AY324811) from the same locality.

In dorsal view, body elliptical (BW 55% of BL), maximal body width attained at the 2/5 of the body (SBW 40% of BL), small constriction at midbody, narrowly rounded snout. In lateral view, body depressed (BW 148% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 71% of BL), broadly rounded snout. Moderately large eyes (ED 11% of BL), not visible from ventral view, positioned high (EH 68% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 30% of BL), moderately wide distance between eyes (IOD 56% of BW). Small rounded nares (ND 1.3% of BL), marked with a marginal rim, positioned moderately high (NH 58% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 61% of NP) and below eye level (NH 86% of EH), wide distance between nares (IND 64% of IOD), reddish region on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 17% of BL), directed posterodorsally, visible from dorsal view and perceivable from lateral view; inner wall free from body and its aperture opens posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 62% of BL), located moderately high on the body (SH 40% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 58% of HAB). Moderately long dextral vent tube (VL 11% of BL), associated with ventral fin, inner wall present. No gland. Short tail (TAL 167% of BL), maximal tail height almost equal to body height (MTH 105% of BH), tail height at midtail equal to body height and almost equal to maximal tail height (THM 100% of BH and 95% of MTH), tail height at the beginning of the tail lower than body height (TH 92% of BH). Moderately developed caudal musculature (TMW 45% of BW, TMH 64% of BH, TMH of 69% of TH and 61% of MTH, TMHM 34% of THM and 33% of MTH). Tail muscle reaches tail tip. Low fins (DF 82% of TMHM, VF 68% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 122% of VF). Dorsal fin originates on the dorsal body-tail junction, keeps straight and almost parallel with tail muscle until proximal 1/4 of the tail, rises regularly to attain it s maximal height and then declines progressively toward the tail tip. Ventral fin originates at the ventral terminus of the body, remains parallel with tail muscle until close to the tail tip where it declines toward the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 43% of TAL), lateral tail vein not visible, myosepta visible on the distal 1/4 of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 70% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip pointed.

Small reduced oral disk (ODW 39% of BW), positioned and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 56% of ODW), gap on the lower labium absent; total number of marginal

papillae 69. Fourty-six submarginal papillae, complete on the lower labium and laterally on upper labium. Short and moderately large conical papillae with rounded tips, longest marginal papillae measured 0.10 mm and 0.15 mm for submarginal papillae, papillae visible from dorsal view. LTRF 3(2-3)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\ len}$ 46% of ODW). Density of keratodonts varies from 27/mm to 45/mm, $A_{1\ den}$ 27/mm (total 25). Wide gap in the first anterior interrupted row (A_{2gap} 65% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_3 scattered. Short indiscernible keratodonts (0.05 mm), poorly keratinized. Distal keratodont same length as those in the middle; prominent space between marginal papillae and keratodont rows. Partially keratinized jaw sheath, edge of the medial convexity black colored and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 47% of ODW) with a long narrowly pointed medial convexity (MCL 31% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.
Coloration in preservative: Generally beige-brownish. Light brown network of melanophores positioned in deep integumental layers and covered major surface of the dorsal sides of the head and trunk and the flank, leaving a slightly transparent lateral area under the skin. Dark brown spots grouped to form patches which scatter on the dorsum skin. Region between the vertebral area and the dorsolateral abdominal wall provided by many brown distinct irregular blotches making the vertebral area detectable. Laterally, jugal area and flank covered by dark brown distinct irregular blotches which group to form slightly dense reticulations leaving a perceptible transparent spiracle above the recognizable intestinal coils. Lower part of the flank not pigmented. Dark roughly distinct irregular brown blotches form irregularly scattered networks on the tail musculature which expand on dorsal fin. Ventral fin pale with few spots closed to tail tip. Ventrally, oral disk, gular and branchial regions beige, abdominal surface transparent, intestinal coils well visible and regularly spiral shaped.
Variation: Four voucher specimens attributed to *M. zolitschka* (ZSM 1741/2007-ZCMV 3436, ZSM 1759/2007-ZCMV 3455, ZSM 1768/2007-ZCMV 3464, ZSM 1841/2007-ZCMV 3563) from the same locality show the typical oral disk configuration and the pigmentatation of this species and one tadpole has a LTRF of 2(2)/3(1-2).

Mantidactylus argenteus Methuen 1920

The following description refers to one tadpole in developmental stage 27 (field number ZCMV 3575-ZSM 1573/2007, BL 12.2 mm, TL 34 mm) from the stream Andohan'i Sity (transect 3) in An'Ala forest.
In dorsal view, body elliptical (BW 47% of BL), maximal body width at mid-body (SBW 50% of BL), narrowly rounded snout with protuberation. In lateral view, body depressed (BW 111% of BH), maximal body height between the proximal 2/5 and 3/5 of the body (SBH 56% of BL), narrowly rounded snout. Small eyes (ED 9% of BL), not visible from ventral view, positioned moderately high (EH 58% of BH) dorsally and directed laterally, situated between the proximal 2/10 and 3/10 of the body (SE 21% of BL), wide distance between eyes (IOD 63% of BW). Very small elliptical nares (ND 0.8% of BL), marked with a marginal rim, positioned moderately high (NH 48% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 68% of NP) and below eye level (NH 84% of EH), moderately wide distance between nares (IND 54% of IOD), red colored region on the back of the nares present, ornamentation absent. Very short sinistral spiracle (SL 9% of BL), directed posteriorly, visible from dorsal and ventral views, perceivable from lateral view; inner wall free from body and its aperture opens posteriorly, eliptical opening, situated between the proximal 2/5 and 3/5 of the body (SS 55% of BL), located moderately high on the body (SH 49% of BH) and below the point where the axis of the tail myotomes contacts the body (SH 77% of HAB). Moderately long dextral vent tube (VL 14% of BL), attached to ventral fin, inner wall present. No gland. Short tail (TAL 180% of BL), maximal tail height higher than body height (MTH 106% of BH), tail height at midtail almost equal to body height and lower than maximal tail height (THM 97% of BH and 82% of MTH), tail height at the beginning of the tail lower than body height (TH 84% of BH). Moderately developed caudal musculature (TMW 60% of BW, TMH 67% of BH, TMH of 80% of TH and 63% of MTH, TMHM 55% of THM and 51% of MTH). Tail muscle reaches tail tip. Very low fin type (DF 43% of TMHM, VF 41% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 104% of VF). Dorsal fin originates on tail muscle on the proximal 1/10 of the tail, remains almost parallel with the tail muscle up to the ¼ of the tail, where it increases abruptly to attain its maximal height and then progresses horizontally until the 3/4 of the tail, finally decreases gradually towards the tail tip. Ventral fin originates at the ventral terminus of the body, remains parallel with tail muscle almost to tail tip, then decreases to tail tip. Maximal tail height located between the proximal 1/5 and 2/5 of the tail (DMTH 37% of TAL), lateral tail vein invisible and myosepta slightly all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 64% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded. Small reduced oral disk (ODW 31% of BW), positioned ventrally and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a wide gap on the upper labium (DG 62% of ODW), gap on the lower labium absent; total number of marginal papillae 31. Eighteen submarginal papillae on the lower labium and laterally on upper labium. Short and moderately wide conical papillae with rounded tips, longest marginal papillae measured 0.15 mm and 0.07 mm for submarginal papillae, papillae not visible from dorsal view. LTRF 2(2)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Long A_1 row ($A_{1\ len}$ 65% of ODW). Density of keratodonts varies

from 26/mm to 36/mm, $A_{1\ den}$ 36/mm (total 41). Wide gap in the first anterior interrupted row (A_{2gap} 63% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_2 and P_3 scattered. Short discernible keratodonts (0.06 mm). Distal keratodonts have the same lengths as those in the middle; prominent space between marginal papillae and keratodont rows. Partially keratinized upper jaw sheath, edge of the medial convexity black colored and the rest whitish; finely pointed serrations; moderately wide jaw sheath (JW 43% of ODW) with a long narrowly pointed medial convexity (MCL 33% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.
Coloration in preservative: Generally brown, dorsally marked by transversal clear bands between nares and eyes, between eyes and spiracle and before the body-tail junction, and a longitudinal clear band on the dorsum of the tail. Brown melanic pigment positioned in deeper dermal layers, separated from a (possibly epidermal) transparent outer skin layer, covering the dorsum and flank of the body. Some dark brown patches scattered on the dorsal skin. Laterally, jugal area (under eyes and nares) and flank covered by dark brown reticulations. The spiracle is reticulated at the base and transparent at the end, and detectable, and is situated the visible intestinal coils. Lower part of the flank not pigmented. Tail musculature overlain by dark brown reticulations. Fins pale, dorsal and ventral fins free from pigments. Ventrally, oral disk, gular and branchial regions patched; venter pale, intestinal coils perceptible and regularly spiral shaped.
Variation: Two voucher specimen (ZSM 1815/2007-ZCMV 3516, ZSM 1849/2007-ZCMV 3566) from the same locality show similar oral disk configuration and coloration pattern.

Mantidactylus sp. 42
(CCS from Montagne d'Ambre)

The following description refers to one tadpole in developmental stage 28 (field number FG/MV 2002.1957-ZSM 774/2004, BL 11.1 mm, TL 34.8 mm) from a stream crossing the the track 'Voie des milles arbres' at the Montagne d'Ambre National Park. The 16S rDNA sequence of this specimen was 99.8% identical to a reference sequence of an adult specimen of *Mantidactylus* sp. 42 (accession FJ559267) from the same locality.
In dorsal view, body elliptical (BW 56% of BL), maximal body width between the proximal 3/5 and 4/5 of the body (SBW 71% of BL), narrowly rounded snout. In lateral view, body depressed (BW 123% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 68% of BL), broadly rounded snout. Moderately large eyes (ED 11% of BL), not visible from ventral view, positioned high (EH 67% of BH) dorsally and directed laterally, situated between the proximal 2/10 and 3/10 of the body (SE 28% of BL), moderately wide distance between eyes (IOD 55% of BW). Small elliptical nares (ND 1.1% of BL), marked with a marginal rim, positioned moderately high (NH 47% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 57% of NP) and below eye level (NH 70% of EH), moderately wide distance between nares (IND 57% of IOD), dark spot on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 15% of BL), directed posteriorly, visible from dorsal and ventral views, perceptible from lateral view; inner wall free from body and its aperture opens laterally instead of posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 62% of BL), located moderately high on the body (SH 55% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 90% of HAB). Moderately long dextral vent tube (VL 13% of BL), attached to ventral fin, inner wall present. No gland. Moderately long tail (TAL 214% of BL), maximal tail height lower than body height (MTH 72% of BH), tail height at midtail higher than body height and lower than maximal tail height (THM 104% of BH and 98% of MTH), tail height at the beginning of the tail almost equal to body height (TH 96% of BH). Moderately developed caudal musculature (TMW 62% of BW, TMH 72% of BH, TMH of 75% of TH and 67% of MTH, TMHM 58% of THM, and 57% of MTH). Tail muscle reaches tail tip. Very low fins (DF 40% of TMHM, VF 45% of MTHM), dorsal fin lower than ventral fin at mid-tail (DF 87% of VF). Dorsal fin originates at the dorsal body-tail junction, rises gradually to attain the maximal height before the midtail and then descents slightly towards the tail tip. Ventral fin originates at the ventral terminus of the body, expands until midtail, and then decreases towards the tail tip. Maximal tail height located at the 2/5 of the tail (DMTH 40% of TAL), lateral tail vein visible only on the proximal 1/3 of the tail, myosepta visible on the proximal ¾ of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 62% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.
Small reduced oral disk (ODW 36% of BW), positioned ventrally and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 47% of ODW), gap on the lower labium absent; total number of marginal papillae 53. Fourty-two submarginal papillae complete on the lower labium and laterally on upper labium. Short and moderately large conical papillae with rounded tips, longest marginal papillae measured 0.13 mm, and 0.14 mm for submarginal papillae, papillae visible from dorsal view. LTRF 3(2-3)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Short A_1 row ($A_{1\ len}$ 33% of ODW). Density of keratodonts varies from 16/mm to 54/mm, $A_{1\ den}$ 16/mm (total 12). Very wide gap in the first anterior interrupted row (A_{2gap} 81% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_2 and P_3 scattered. Short discernible keratodonts (0.09 mm). Distal keratodonts have the same lengths as those in the middle; important space between marginal papillae and keratodont rows.

Partially keratinized jaw sheath, edge of the medial convexity black colored and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 51% of ODW) with a short widely rounded medial convexity (MCL 18% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.
Coloration in preservative: Generally brownish. Brown pigments in deep integumental layers covering the dorsum and flank of the body, leaving out a narrow slightly transparent area laterally. Dark brown patches of melanophores scattered on the skin. Rather unpigmented surface on the dorsum between the body wall and the vertebral area perceivable. Irregularly shaped clear dots form a line which runs on the dorsolateral part of the abdominal region, from the body-tail junction to just behind the eyes. There it splits, the first ramification passes below the eyes and runs through the jugal area, then diverts laterally on the sagittal plan of the nares. The second ramification runs above the eyes and approaches the first line of spots on the sagittal plan of the nares and finally merges with it on the snout. Laterally, jugal area and flank covered by dark brown dense reticulation leaving a perceivable opaque reticulated spiracle. Lower part of the flank clear, intestinal coils recognizable. A line formed by irregularly shaped clear dots is visible laterally before the body-tail junction, runs on the dorsolateral part of the abdominal region and splits just behind the eyes. The first ramification passes below the eyes and ends below the nares. The second ramification passes above the eyes and the nares and teminates on the mid-height of the snout. Tail musculature pinkish with brown mottles which coalesce to form rather dense reticulations especially on the dorsolateral part. Fins speckled, dorsal fin patched, some blotches on the ventral fin close to tail tip. Ventrally, oral disk, gular and branchial regions reticulated; venter pale, intestinal coils perceptible and regularly spiral shaped.

Mantidactylus sp. 43
(CCS from Marojejy)

The following description refers to one tadpole in developmental stage 25 (field number FGZC 2928-ZSM 1610/2007, BL 7 mm, TL 21 mm) from a stream crossing the way to the Cascade in Camp Mantella at the Marojejy National Park. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult specimen of *Mantidactylus* sp. 43 (accession FJ559268) from the same locality.
In dorsal view, body elliptical (BW 60% of BL), maximal body width attained between the proximal 2/5 and 3/5¾ of the body (SBW 54% of BL), narrowly rounded snout. In lateral view, body depressed (BW 142% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 71% of BL), broadly rounded snout. Moderately large eyes (ED 13% of BL), not visible from ventral view, positioned high (EH 78% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 39% of BL), moderately wide distance between eyes (IOD 59% of BW). Small rounded nares (ND 2% of BL), marked with a marginal rim, positioned high (NH 65% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 76% of NP) and below eye level (NH 84% of EH), moderately wide distance between nares (IND 58% of IOD), dark spot on the back of the nares absent, ornamentation absent. Short sinistral spiracle (SL 15% of BL), directed posteriorly, visible from dorsal and ventral views and perceptible from lateral view; inner wall free from body and its aperture opens posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 75% of BL), located moderately high on the body (SH 52% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 85% of HAB). Short dextral vent tube (VL 7% of BL), attached to ventral fin, inner wall present. No gland. Short tail (TAL 200% of BL), maximal tail height higher than body height (MTH 107% of BH), tail height at midtail higher than body height but lower than maximal tail height (THM 107% of BH and 93% of MTH), tail height at the beginning of the tail lower than body height (TH 94% of BH). Moderately developed caudal musculature (TMW 49% of BW, TMH 64% of BH, TMH of 68% of TH and 58% of MTH, TMHM 51% of THM and 50% of MTH). Tail muscle reaches tail tip. Very low fins (DF 57% of TMHM, VF 39% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 148% of VF). Dorsal fin originates at dorsal body-tail junction, increases to attain the maximal height before the midtail and then descents slightly towards the tail tip. Ventral fin originates at the ventral terminus of the body, continues straight until the ¾ of the tail, and then declines towards the tail tip. Maximal tail height located between the proximal 1/5 and 2/5 of the tail (DMTH 31% of TAL), lateral tail vein visible only on the proximal 1/4 of the tail, myosepta visible all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 60% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.
Moderately wide reduced oral disk (ODW 46% of BW), positioned and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 54% of ODW), gap on the lower labium absent; total number of marginal papillae 78. Fifty submarginal papillae, complete on the lower labium and laterally on upper labium. Very short and moderately large conical papillae with rounded tips, longest marginal papillae measured 0.10 mm and 0.08 mm for submarginal papillae, papillae visible from dorsal view. LTRF 2(2)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\,len}$ 51% of ODW). Density of keratodonts varies from 13/mm to 63/mm, $A_{1\,den}$ 13/mm (total 13). The first upper row seems to have lost many of its keratodonts. Wide gap in the first anterior interrupted row (A_{2gap} 66% of A_2). Rows alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted.

Short discernible keratodonts (0.07 mm). Distal keratodont have same length as those in the middle; prominent space between marginal papillae and keratodont rows. Partially keratinized jaw sheath, edge of the medial convexity black colored and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 41% of ODW) with a moderately long widely pointed medial convexity (MCL 26% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper ones.
Coloration in preservative: Uniformly pale. Body and tail muscle dorsally flecked. Speckles in deeper dermal layers, separately from externalmost (possibly epidermal) skin layer. Darker patches dissipate between the eyes and along the vertebral area; brown irregularly shaped spots dispersed on the dorsal skin. Intestinal coils noticeable on the lateral part of the abdomen. Laterally, jugal area and flank covered by dark sparse brown melanophoric spots, leaving out an opaque, slightly blotched area around spiracle, above the detectable intestinal coils. Lower part of the flank unpigmented. Tail musculature beige with brown distinct mottles which group in some areas to form sporadic patches that extend onto the dorsal fin and their density diminishes towards tail tip. Fins translucent, speckled, especially on the proximal 1/4 of the dorsal fin; brown fused mottles abundant on dorsal fin and scattered mottles on the ventral fin. Ventrally, oral disk, gular and branchial regions beige, sporadically spotted; venter transparent, intestinal coils conspicuous and regularly spiral shaped.

Mantidactylus sp. 47
(CCS from Ambatolahy and other sites around Ranomafana)

The following description refers to one tadpole in developmental stage 31 (field number ZCMV 2699-ZSM 456/2008, BL 12.1 mm, TL 32.1 mm) from Imaloka river at the Ranomafana National Park. The 16S rDNA sequence of this specimen was 99.8% identical to a reference sequence of an adult specimen of *Mantidactylus* sp. 47 (accession FJ559272) from the same locality.
In dorsal view, body elliptical (BW 52% of BL), maximal body width attained between the proximal 3/5 and 4/5 of the body (SBW 69% of BL), constriction before the point where the maximal body width is attained, narrowly rounded snout. In lateral view, body depressed (BW 130% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 69% of BL), broadly rounded snout. Moderately large eyes (ED 13% of BL), not visible from ventral view, positioned high (EH 73% of BH) dorsally and directed dorsolaterally, situated between the proximal 2/10 and 3/10 of the body (SE 26% of BL), moderately wide distance between eyes (IOD 59% of BW). Small rounded nares (ND 1.1% of BL), marked with a marginal rim, positioned moderately high (NH 53% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 48% of NP) and below eye level (NH 72% of EH), moderately wide distance between nares (IND 58% of IOD), dark spot on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 14% of BL), directed posterodorsally, not visible from either dorsal or ventral view, perceivable from lateral view; inner wall free from body and its aperture opens posteriorly, rouded opening situated between the proximal 2/5 and 3/5 of the body and almost at midbody (SS 55% of BL), located moderately high on the body (SH 51% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 76% of HAB). Moderately long dextral vent tube (VL 11% of BL), attached to ventral fin, inner wall present. No gland. Short tail (TAL 166% of BL), maximal tail height equal to body height (MTH 100% of BH), tail height at midtail lower than body height and maximal tail height (THM 90% of BH and 93% of MTH), tail height at the beginning of the tail lower than body height (TH 90% of BH). Developed caudal musculature (TMW 63% of BW, TMH 73% of BH, TMH of 81% of TH and 73% of MTH, TMHM 67% of THM and 62% of MTH). Tail muscle reaches tail tip. Very low fins (DF 28% of TMHM, VF 24% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 117% of VF). Dorsal fin originates on the proximal 1/5 of the tail, rises gradually and then progresses horizontally to the tail tip, then decreases. Ventral fin originates at the ventral terminus of the body, remains parallel with tail muscle almost to tail tip, then decreases. Maximal tail height located at the 2/5 of the tail (DMTH 40% of TAL), lateral tail vein visible only on the proximal 1/4 of the tail, myosepta slightly visible all along the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 67% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.
Small reduced oral disk (ODW 36% of BW), positioned and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae interrupted by a moderately wide gap on the upper labium (DG 44% of ODW), gap on the lower labium absent; total number of marginal papillae 72. Sixty-six submarginal papillae complete on the lower labium and laterally on upper labium. Short and moderately large conical papillae with rounded tips, longest marginal papillae measured 0.14 mm and 0.11 mm for submarginal papillae, papillae not visible from dorsal view. LTRF 3(2-3)/3(1-2) after Altig and McDiarmid (1999). Single row of keratondonts per ridge. Moderately long A_1 row ($A_{1\,len}$ 42% of ODW). Density of keratodonts varies from 15/mm to 40/mm, $A_{1\,den}$ 15/mm (total 14). Wide gap in the first anterior interrupted row (A_{2gap} 76% of A_2). Row alignment irregular, lower keratodont rows form a chevron, P_1 and P_2 interrupted, P_3 scattered. Short discernible keratodonts (0.05 mm). Distal keratodont same length as those in the middle; important space between marginal papillae and keratodont rows. Partially keratinized jaw sheath, edge of the medial convexity black colored and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 51% of ODW) with a moderately long widely pointed medial convexity (MCL 20% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.

Coloration in life: Typically light brownish with irregular variegated pattern. Dorsal skin irregularly covered by brown melanophores and some gold iridophoric spots or patches. Dorsolaterally and laterally with the same pattern as dorsally. Rather non-pigmented spiracle perceptible. Tail musculature yellowish with roughly distinct, irregular brown blotches that group to form irregular patches. Their density diminues towards the tail tip. Sporadic golden iridopohoric spots perceptible. Fins translucent, dorsal fin with many dark patches, ventral fin unpigmented. Ventrally, oral disk and gular region not pigmented and bordered by a reticulated body wall; branchial area reddish, gills and beating heart visible; venter transparent, intestinal coils visible and regularly spiral shaped.
Coloration in preservative: Largely brownish. Brown flecks in deep integumental layers cover the dorsum and condense mainly on the vertebral area and the very dark abdominal part. Light brown flecks dispersed on the skin. Roughly distinct irregular brown blotches grouped to form irregularly scattered networks, largely between the eyes and between the vertebral area and the abdominal region. Noticeable transversal lines occur between the vertebral area and the abdominal region showing noticeable abdominal-like structure. Laterally, jugal area and flank covered by irregular brown blotches which fuse to form networks mainly below the nares and between the eyes, and on the abdominal surface leaving a spotted spiracle diverged above the discernible intestinal coils. Lower part of the flanks not pigmented. Tail musculature beige with roughly distinct irregular brown blotches that group to form irregular patches. Their density diminishes towards the tail tip. Fins translucent, dorsal fin with many patches, ventral fin unpigmented. Ventrally, oral disk and gular region beige and bordered by a reticulated body wall; venter pale, intestinal coils visible and regularly spiral shaped.
Variation: Five voucher specimens (ZSM 1697/2007-ZCMV 3774, ZSM 254/2008-ZCMV 3669, ZSM 315/2008-ZCMV 3620, ZSM 478/2008-ZCMV 3724, ZSM 506/2008-ZCMV 3791) attributed to this species from the same locality and many non-voucher specimens belonging to these series indicate the identical oral disk configuration and the external pigmentation of this species. Only the LTRF is variable: 2(2)/3(1-2) and 3(2-3)/3(2-3).

Mantidactylus mocquardi Angel 1929

The following description refers to one tadpole in developmental stage 26 (field number ZCMV 3511-ZSM 1540/2007, BL 11.4 mm, TL 32.5 mm) from the stream Andohan'i Sity (transect 2) in An'Ala forest. The 16S rDNA sequence of this specimen was 99.3% identical to a reference sequence of an adult specimen of *M. mocquardi* (accession FJ559269; ZCMV 5865; referred to as *Mantidactylus* sp. 44 by Vieites *et al.*, 2009) from Ambohitsara-Tsitolaka.
In dorsal view, body elliptical (BW 60% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 47% of BL), narrowly rounded snout. In lateral view, body depressed (BW 148% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 73% BL), broadly rounded snout. Moderately large eyes (ED 12% of BL), not visible from ventral view, positioned high (EH 73% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 35% of BL), moderately wide distance between eyes (IOD 53% of BW). Small rounded nares (ND 1.4% of BL), marked with a marginal rim, positioned dorsally moderately high (NH 59% of BH) and oriented anterodorsolaterally, situated nearer to snout than to eye (RN 67% of NP) and below eye level (NH 81% of EH), wide distance between nares (IND 68% of IOD), reddish region on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 16% of BL), directed posteriorly, visible from dorsal, ventral and lateral views; inner wall free from body and formed such that aperture opens laterally instead of posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 68% of BL), located moderately high on the body (SH 42% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 70% of HAB). Short dextral vent tube (VL 9% of BL), attached to ventral fin, inner wall present. No gland. Short tail (TAL 185% of BL), maximal tail height equal to body height (MTH 102% of BH), tail height at midtail lower than body height, but equal to maximal tail height (THM 91% of BH and 99% of MTH), tail height at the beginning of the tail lower than body height (TH 91% of BH). Developed caudal musculature (TMW 51% of BW, TMH 74% of BH, TMH of 81% of TH and 73% of MTH, TMHM 60% of THM and 60% of MTH). Tail muscle reaches tail tip. Very low fins (DF 41% of TMHM, VF 25% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 161% of VF). Dorsal fin originates on the proximal 1/3 of the tail, rises suddenly up to its maximal height, then progresses parallel with caudal musculature, then decreases towards the tail tip at the proximal 1/4 of the tail. Ventral fin originates at the ventral terminus of the body, remains almost parallel with tail muscle up to almost tail tip, then decreases. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 42% of TAL), lateral tail vein not visible, myosepta visible on the distal ¾ of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 60% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip pointed.
Moderately wide reduced oral disk (ODW 43% of BW), positioned and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae, gap on the upper and lower labium absent; total number of marginal papillae 74. One hundred and four submarginal papillae complete on the lower labium and laterally on upper labium. Moderately long and large elongated papillae with rounded tips on the marginal papillae and pointed tips on the submarginal papillae. Longest marginal papillae measured 0.19 mm and 0.25 mm for submarginal papillae, papillae visible from dorsal view. Keratodonts absent. Partially keratinized jaw

sheath, only the edge of the medial convexity is weakly brown colored and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 43% of ODW) with a moderately long narrowly pointed medial convexity (MCL 22% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.
Coloration in preservative: Broadly light beige-brownish. Brown blotches in deep integumental layers form dark patches principally along the vertebral area and the abdominal region, leaving out laterally a slightly translucent area. Some dark brown patches scattered irregularly on the skin between nares and eyes, between the eyes, on the jugal area, and on the area between the vertebral and the abdominal area. Light brown flecks spread over the dorsum. Reddish region on the back of the nares present. Laterally, jugal area and flank covered by distinct irregular brown blotches that dissipate on the abdominal region and condense to form sparse networks on the jugal region, mainly on the lateral area between nares and eyes and between the eye and the spiracle, and leaving a visible transparent spiracle diverged above the recognizable intestinal coils. Lower part of the flank spotted. Tail musculature beige with distinct irregular brown blotches which group to form irregularly scattered patches. Their density diminishes towards the tail tip. Fins pale, with brown sporadic patches on the dorsal fin, ventral fin not pigment. Ventrally, oral disk, gular and branchial regions beige; venter transparent, intestinal coils well visible and regularly spiral shaped.
Variation: Nine other voucher specimens (ZSM 1539/2007-ZCMV 3510, ZSM 1541/2007-ZCMV 3513, ZSM 1746/2007-ZCMV 3441, ZSM 1761/2007-ZCMV 3457, ZSM 1771/2007-ZCMV 3469, ZSM 1805/2007-ZCMV 3447, ZSM 1813/2007-ZCMV 3509, ZSM 1844/2007-ZCMV 3567, ZSM 1846/2007-ZCMV 3570) and one voucher specimen from Ambohitsara-Tsitola (ZSM 72/2008-ZCMV 4936) assigned to this species from the same locality reveal the identical oral disk configuration and external pigmentation of this species.

Mantidactylus mocquardi (Mahasoa)

A further description of a tadpole assigned to *M. mocquardi* but with some morphological differences refers to one tadpole in developmental stage 27 (field number ZCMV 8094-ZSM 686/2008, BL 13.8 mm, TL 42.6 mm) from Mahasoa forest. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult specimen of *Mantidactylus mocquardi* (ZCMV 8818) from the same locality, and 99% identical to an adult of *M. mocquardi* from Ambohitsara (accession number FJ559269).
In dorsal view, body elliptical (BW 63% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 48% of BL), narrowly rounded snout. In lateral view, body depressed (BW 136% of BH), maximal body height attained at the distal 1/5 of the body (SBH 81% of BL), broadly rounded snout. Moderately large eyes (ED 13% of BL), not visible from ventral view, positioned high (EH 67% of BH) dorsally and directed dorsolaterally, situated between the proximal 3/10 and 4/10 of the body (SE 32% of BL), moderately wide distance between eyes (IOD 54% of BW). Small rounded nares (ND 1.6% of BL), marked with a marginal rim, positioned moderately high (NH 53% of BH) dorsally and oriented anterodorsolaterally, situated nearer to snout than to eye (RN 59% of NP) and below eye level (NH 79% of EH), wide distance between nares (IND 70% of IOD), dark spot on the back of the nares absent, ornamentation absent. Short sinistral spiracle (SL 10% of BL), directed posteriorly, visible from dorsal and ventral views, recognizable from lateral view; inner wall free from body, its aperture opens posteriorly, elliptical opening, situated between the proximal 3/5 and 4/5 of the body (SS 71% of BL), located moderately high on the body (SH 48% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 76% of HAB). Moderately long dextral vent tube (VL 12% of BL), attached to ventral fin, inner wall present. No gland. Moderately long tail (TAL 209% of BL), maximal tail height higher than body height (MTH 109% of BH), tail height at midtail equal to body height and to maximal tail height (THM 97% of BH and 100% of MTH), tail height at the beginning of the tail equal to body height (TH 97% of BH). Developed caudal musculature (TMW 56% of BW, TMH 78% of BH, TMH of 80% of TH and 71% of MTH, TMHM 54% of THM and 54% of MTH). Tail muscle reaches tail tip. Very low fins (DF 52% of TMHM, VF 34% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 154% of VF). Dorsal fin originates at the proximal 1/5 of the tail, rises progressively up to its maximal height and then declines towards the tail tip. Ventral fin originates at the ventral terminus of the body, remains almost parallel with tail muscle almost up to the tail tip, then decreases. Maximal tail height located at midtail (DMTH 50% of TAL), lateral tail vein not visible, myosepta visible on the proximal ¾ of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 63% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip pointed.
Moderately wide reduced oral disk (ODW 47% of BW), positioned and directed ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae, gap on the upper and lower labium absent; total number of marginal papillae 89. Eighty-eight submarginal papillae complete on the lower labium and laterally on upper labium. Long and large elongated papillae with rounded tips on the marginal and pointed tips on the submarginal papillae, longest marginal papillae measured 0.25 mm and 0.35 mm for submarginal papillae, papillae not visible from dorsal view. Two submarginal papillae on the upper labium beside (left and right) the medial convexity project in the same direction as the medial convexity. Keratodonts absent. Partially keratinized jaw sheath, only the edge of the medial convexity is weakly brown colored and the remainder whitish; finely pointed serrations; moderately wide jaw sheath (JW 48%

of ODW) with a very long narrowly pointed medial convexity (MCL 57% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.
Coloration in preservative: Predominantly pale-brownish. Light pale brown melanophoric pigment covered the dorsum and condensed to form dark patches especially between the eyes, on the vertebral and the abdominal area. Some dark brown patches scattered on the skin. Irregularly shaped clear dots form a line which runs on the dorsolateral part of the abdominal regions, from the body-tail junction to just behind the eyes where it splits, the first ramification passes bellow the eyes and runs through the jugal area, before it diverts laterally on the sagittal plan of the nares. The second ramifications pass above the eyes and approach each other on the sagittal plan of the nares and finish to merge in the snout. Laterally, jugal area and flank covered by speckles leaving an conspicuous flecked spiracle on the pale body wall. Lower part of the flanks unpigmented, intestinal coils laterally not visible. The line formed by irregularly shaped clear dots is visible laterally before the body-tail junction. It runs on the dorsolateral part of the abdominal region and splits just behind the eyes. The first ramification passes below the eyes and ends below the nares. The second ramification passes above the eyes and the nares and terminates on the mid-height of the snout. Tail musculature with irregular brown blotches which group to form irregularly scattered patches. Their density diminishes towards the tail tip. Fins pale, dorsal fin with brown spots which group to form patches, sporadic patches spread around tail tip on ventral fin. Ventrally, oral disk, gular and branchial regions beige with brown spots; venter pale, intestinal coils merge under the abdominals-like structure and regularly spiral shaped.
Variation: Four additional specimens belonging to the same series (but not identified by DNA barcoding) and having the same external morphology as the voucher specimen reveal the identical oral disk configuration and morphological parameters.

Mantidactylus sp. 64
(CCS from Namorona and other sites around Ranomafana)

The following description refers to one tadpole in developmental stage 39 (field number ZCMV 2646-ZSM 401/2008, BL 10. 8 mm, TL 31.9 mm) from the Namorona river in front of Hotel Manja in Ranomafana village. The 16S rDNA sequence of this specimen was 96% identical to a reference sequence of an adult specimen of *Mantidactylus* sp. 47 (accession GU975698) from Ambatolahy in the Ranomafana National Park. Since we found morphologically different tadpoles that 100% genetically matched adults of M. sp. 47, we conclude that adults of M. sp. 64 are so far unknown and the CCS status for this species is based on the distinct morphology of tadpoles that are genetically divergent and occur in sympatry with M. sp. 47..
In dorsal view, body elliptical (BW 59% of BL), maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 48% of BL), narrowly rounded snout. In lateral view, body depressed (BW 136% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 69% of BL), narrowly rounded snout. Moderately large eyes (ED 13% of BL), not visible from ventral view, positioned high (EH 79% of BH) dorsally and directed dorsolaterally, situated between the proximal 2/10 and 3/10 of the body (SE 27% of BL), moderately wide distance between eyes (IOD 64% of BW). Small rounded nares (ND 1.3% of BL), marked with a marginal rim, positioned high (NH 62% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 59% of NP) and below eye level (NH 79% of EH), wide distance between nares (IND 70% of IOD), dark spot on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 10% of BL), directed posteriorly, visible from dorsal and ventral view and perceptible from lateral view; inner wall free from body and formed such that aperture opens laterally instead of posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 71% of BL), located moderately high on the body (SH 54% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 76% of HAB). Moderately long dextral vent tube (VL 12% of BL), attached to ventral fin, inner wall present. No gland. Moderately long tail (TAL 209% of BL), maximal tail height higher than body height (MTH 109% of BH), tail height at midtail equal to body height and maximal tail height (THM 97% of BH and 100% of MTH), tail height at the beginning of the tail lower than body height (TH 97% of BH). Moderately developed caudal musculature (TMW 56% of BW, TMH 78% of BH, TMH of 72% of TH and 71% of MTH, TMHM 54% of THM and 54% of MTH). Tail muscle reaches tail tip. Very low fins (DF 52% of TMHM, VF 34% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 117% of VF). Dorsal fin originates at the proximal 1/10 of the tail, rises gradually to attend its maximal height before mid tail and then progresses horizontally up to the distal 1/5 of the tail, where it decreases. Ventral fin originates at the ventral terminus of the body, remains parallel with tail muscle almost up to the tail tip, where it decreases. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 42% of TAL), lateral tail vein not visible, myosepta slightly visible on the proximal 1/4 of the tail musculature, point where the axis of the tail myotomes contacts the body in the upper half of the body height (HAB 70% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.
Moderately wide reduced oral disk (ODW 47% of BW), positioned ventrally and directed anteroventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, upper labium is a continuation of snout. Single row of marginal papillae, gap on the upper and lower labium absent; total number of marginal papillae 81. Eighty-seven submarginal papillae complete on the lower labium and laterally on upper labium. Short and moderately large conical papillae with rounded tips, longest marginal papillae measured 0.11 mm and 0.15 mm for submarginal papillae, papillae not visible from dorsal view. Keratodonts absent. Partially keratinized jaw sheath, edge of the medial convexity weakly brown colored and the remainder

whitish; finely pointed serrations; moderately wide jaw sheath (JW 55% of ODW) with a moderately long widely rounded medial convexity (MCL 21% of JW). Lower jaw sheath V-shaped, partially keratinized and totally hidden by the upper jaw sheath.
Coloration in life: Typically reddish-brown. Body and tail covered by brown blotches which condense and give a dark brown coloration to the tadpole. Golden irridophoric pigments spread over the skin. Dorsolaterally and laterally identical to the dorsal pattern. Rather non-pigmented spiracle perceptible. Tail musculature yellowish with roughly distinct, irregular brown blotches condensed to form networks. Their density extends towards the tail tip. Fins translucent, dorsal fin provided by some dark patches and ventral fin unpigmented. Ventrally, oral disk and gular and branchial reticulated, gills and beating heart perceptible; venter transparent, intestinal coils visible and regularly spiral shaped.
Coloration in preservative: Largely dark. Brown melanophoric pigment covering the skin gave almost uniform dorsal coloration; merged light patches occurred between the eyes, on the vertebral area and on the abdominal region. Sparse dark mottles dispersed mainly on the back of the nares between the eyes and on the dorsum, condensed on the dorsolateral part of the abdomen closed to the body-tail junction to form networks. Perceivable transversal lines occur between the vertebral area and the abdominal region showing noticeable abdominals-like structure. Irregularly shaped roughly clear dots form a line that runs on the dorsolateral part of the abdominal region, from the body-tail junction to just behind the eyes where it splits, the first ramification passes bellow the eyes and goes through the jugal area, until diverting laterally close to the sagittal plan of the nares. The second ramification passes above the eyes and fades off on the anterior limit of the eyes. Laterally, jugal area and flank covered by dense dark brown melanophoric reticulations leaving a noticeable reticulated spiracle diverged above intestinal coils. Lower part of the flanks unpigmented. The line formed by the irregularly shaped clear dots is conspicuous laterally, before the body-tail junction, runs on the dorsolateral part of the abdominal region and splits just behind the eye, the first ramification passes below the eyes and ends below the nares. The second ramification passes above the eye and fades at the anterior limit of the eye. Tail musculature pale and covered by dark brown reticulations. Their density increases towards the tail tip. Fins pale, with brown reticulations close to the tail tip. First part of dorsal fin mottled. Ventrally, oral disk reticulated, gular and branchial regions patched; venter pale, intestinal coils perceptible and regularly spiral shaped.
Variation: The picture of one uncataloged voucher specimen (ZCMV 9291) from Sakaroa in Ranomafana National Park, designated to this species, displays the same external pigmentation. The examination of its oral disk is not possible due to the unavaibility of this specimen.

Mantidactylus majori Boulenger 1896

The following description refers to one tadpole in developmental stage 29 (field number ZCMV 3761-ZSM 1684/2004, BL 11.4 mm, TL 36.9 mm) from the Sahamalaotra stream in the Ranomafana National Park. The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of an adult specimen of *Mantidactylus majori* (accession AY848187) from the same locality.
In dorsal view, body elliptical (BW 64% of BL), maximal body width attained almost at midbody (SBW 49% of BL), narrowly rounded snout. In lateral view, body depressed (BW 147% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 68% of BL), broadly rounded snout. Large eyes (ED 15% of BL), not visible from ventral view, positioned high (EH 78% of BH) dorsally and directed laterally, situated between the proximal 3/10 and 4/10 of the body (SE 38% of BL), wide distance between eyes (IOD 66% of BW). Moderately large elliptical nares (ND 2.5% of BL), marked with a marginal rim, positioned high (NH 64% of BH) dorsally and oriented anterolaterally, situated nearer to snout than to eye (RN 59% of NP) and below eye level (NH 81% of EH), moderately wide distance between nares (IND 54% of IOD), dark spot on the back of the nares present, ornamentation absent. Short sinistral spiracle (SL 16% of BL), directed posteriorly, visible from dorsal and ventral view, conspicuous from lateral view; inner wall free from body and its aperture opens posteriorly, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 76% of BL), located low on the body (SH 38% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 61% of HAB). Moderately long medial vent tube with lateral displacement (VL 11% of BL), attached to ventral fin. No gland. Short tail (TAL 181% of BL), maximal tail height equal to body height (MTH 101% of BH), tail height at midtail lower than body height and maximal tail height (THM 94% of BH and 93% of MTH), tail height at the beginning of the tail lower than body height (TH 88% of BH). Moderately developed caudal musculature (TMW 26% of BW, TMH 70% of BH, TMH of 79% of TH and 69% of MTH, TMHM 56% of THM and 52% of MTH). Tail muscle reaches tail tip. Very low fins (DF 52% of TMHM, VF 27% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 195% of VF). Dorsal fin originates at the dorsal body-tail junction, progresses horizontally until the 1/4 of the tail, then ascends abruptly to attain the maximal height before the midtail, progresses more or less horizontally until the ¾ of the tail, then decreases abruptly towards the tail tip. Ventral fin originates at the ventral terminus of the body, continues parallel with the caudal musculature until midtail, and then decreases continuously towards the tail tip. Maximal tail height located between the proximal 2/5 and 3/5 of the tail (DMTH 41% of TAL), lateral tail vein not visible, myosepta slightly visible on the proximal 3/4 of the tail musculature, point where the axis of the tail myotomes contacts

the body in the upper half of the body height (HAB 62% of BH), axis of the tail myotomes parallel with the axis of the trunk. Tail tip narrowly rounded.
Moderatly wide highly modified oral disk (ODW 40% of BW), positioned and directed ventrally, not emarginated, maximal width in the middle. Oral disk not visible from dorsal view, anterior margin is separated with the snout by a shallow crevice. Single row of marginal papillae, gap on the upper and lower labium absent; total number of marginal papillae 72. One hundred and thirty-five submarginal papillae complete on the lower labium and upper labium. Very long and very large elongated papillae with pointed tips, longest marginal papillae measured 0.25 mm and 0.41 mm for submarginal papillae, papillae not visible from dorsal view. Keratodonts absent. Moderately wide jaw sheath (JW 54% of ODW), upper jaw sheath transformed into three immense flexible slightly curved thorn-shaped papillae (right 0.56 mm, middle 0.81 mm, left 0.66 mm). A similar papilla is situated laterally to the bases of the two outer papillae. 12 large papillae project from near the base of what appears to be a non-pigmented, non-keratinized, non-serrated lower jaw sheath, which is totally hidden by the upper ones.
Coloration in life: Broadly yellowish-orange with brown patches. Brown melanophoric patches in deep integumental layers extended especially between the eyes and on the vertebral region. Dark brown to black melanophoric patches spread sporadically over the skin, golden iridophoric mottles group to form irregular patches mainly on the dorsum. Laterally, body wall overlain by dark patches of melanophores on the jugal region, below the eye and between the eye and the spiracle. Partly reticulated transparent spiracle diverged on the dark abdominal wall. Blotches of iridophores scattered irregularly. Tail musculature orange-yellowish with brown dots forming irregularly scattered patches. Fins translucent, dorsal fin with scattered patches, ventral fin almost unpigmented. Lateral tail vein reddish. Ventrally, oral disk and gular region yellowish; branchial regions reddish, gills and beating heart clearly visible; abdominal surface transparent with golden iridophoric patches, intestinal coils visible and regularly spiral shaped.
Coloration in preservative: Generally beige. Brown patches in deep integumental layers extend between eyes and nares, between the eyes, on the vertebral and abdominal areas, leaving out laterally a slightly transparent area. Light brown flecks cover the dorsal surface and dark brown blotches dissipate irregularly on the dorsal skin. Laterally, jugal area and flank covered by irregular brown blotches that are sparsely spread and that condense to form sparse networks mainly on the lateral area between nares and eyes, and between the eye and the spiracle, leaving out a visible opaque spiracle diverged above the visible intestinal coils. Lower part of the flank not pigmented. Tail musculature orange-yellowish with brown dots consolidated to form irregularly scattered patches. Fins translucent, dorsal fin with scattered patches, ventral fin amost unpigmented. Ventrally, oral disk, gular and branchial regions beige; venter transparent, intestinal coils visible and regularly spiral shaped.
Variation: 32 other voucher specimens (ZSM 42/2007-ZCMV 4155, ZSM 93/2007-ZCMV 4132, ZSM 335/2007-T 172, ZSM 379/2007-ZCMV 4235, ZSM 495/2007-ZCMV 4699, ZSM 502/2007-ZCMV 4517, ZSM 609/2007-T 410, ZSM 682/2007-ZCMV 5391, ZSM 954/2007-ZCMV 5979, ZSM 1062/2007-T 32, ZSM 1063/2007-T 168, ZSM 1078/2007-T 38, ZSM 1285/2007-ZCMV 4417, ZSM 1328/2007-T 156, ZSM 1382/2007-ZCMV 4534, ZSM 1653/2007-ZCMV 3722, ZSM 1676/2007-ZCMV 3749, ZSM 1684/2007-ZCMV 3761, ZSM 1699/2007-ZCMV 3776, ZSM 1700/2007-ZCMV 3777, ZSM 1701/2007-ZCMV 3778, ZSM 171/2008-ZCMV 3806, ZSM 202/2008-ZCMV 3835, ZSM 203/2008-ZCMV 3836, ZSM 229/2008-ZCMV 3627, ZSM 256/2008-ZCMV 3672, ZSM 429/2008-ZCMV 2674, ZSM 441/2008-ZCMV 2686, ZSM 447/2008-ZCMV 2694, ZSM 445/2008-ZCMV 2690, ZSM 455/2008-ZCMV 2698, ZSM 473/2008-ZCMV 3704) from the same locality and one voucher specimen from Vevembe forest (ZSM 1384/2004-TAD 6 Vevembe) attributed to this species reveal the identical oral disk configuration, external pigmentation and other morphological parameters.

Gephyromantis granulatus (Boettger 1881)

The following description refers to one tadpole in developmental stage Gosner 40 Field number Tad 2004–75 - ZSM 298/2008, BL 5.8 mm, TL 20.7 mm) collected by R.D. Randrianiaina, M. Puente, and F. Glaw on 19-23 February 2004 in Montagne d'Ambre National Park in a brook crossing the track "Voie des milles arbres" (coordinates at stream not taken, but not far from 12°31.667'S, 49°10.667'E, 1050 m a. s. l.). The 16S rDNA sequence of this specimen was 100% identical to the reference sequence of a *G. granulatus* adult specimen (accession AJ315926) in Genbank.
In dorsal view, body ovoid, maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 44% of BL), broadly rounded snout. In lateral view, body depressed (BW 132% of BH), maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 62% of BL), rounded snout. Large eyes (ED 17% of BL), visible from ventral view, positioned high (EH 61% of BH) laterally and directed laterally, situated between the proximal 2/10 and 3/10 of the body (SE 25% of BL), wide distance between eyes (IOD 68% of BW). Small round nares (ND 1.4% of BL), countersunk, positioned low (NH 33% of BH) laterally and oriented ventrally, situated nearer to snout than to eye (RN 42% of NP) and lower than the eye (NH 55% of EH), moderately wide distance between nares (IND 56% of IOD), dark spot on the back of the nares absent, ornamentation absent. Moderately large sinistral spiracle (SL 14% of BL), directed posteriorly, visible from ventral view, and conspicuous from lateral view; inner wall absent and its aperture opens posteriorly; elliptical opening, situated between the proximal 2/5 and 3/5 of the body (SS 60% of BL), located low on the body (SH 39% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 61% of HAB). Moderately long medial vent tube (VL 14% of BL), not attached to the ventral fin. No glands. Very long tail (TAL 305% of BL), maximal tail height higher than body height (MTH 115% of BH), tail height at midtail higher than body height but lower than maximal tail height (THM 108% of BH and THM 94% of MTH), tail height at the beginning of the tail lower than body height (TH 66% of BH). Caudal musculature well-

developed (TMW 80% of BW, TMH 66% of BH, TMH 100% of TH and 58% of MTH, TMHM 72% of THM, TMHM 67% of MTH). Tail muscle reaches tail tip. Very low fin (DF 18% of TMHM, VF 23% of MTHM), dorsal fin lower than ventral fin at mid-tail (DF 81% of VF). Dorsal fin originates on the proximal 1/10 of the tail musculature, rises progressively to attain its maximal height at the maximal tail height and then descents slightly towards the tail tip. Ventral fin originates on the caudal musculature just behind the vent tube, ascends gradually to attain its maximal height at the maximal tail height and then declines towards the tail tip. Maximal tail height located between the proximal 3/5 and 4/5 of the tail (DMTH 69% of TAL), caudal vein conspicuous all along the tail, myosepta perceptible on the proximal ½ of the tail musculature, point of contact axis of the tail myotomes with the body located high (HAB 65% of BH), axis of the tail myotomes not parallel with the axis of the trunk. Tail tip narrowly rounded. Very small oral disk (ODW 15% of BW), positioned and directed ventrally, not visible from dorsal view and not connected to the snout. Oral disk opening triangular, lower labium absent and upper labium folded to form a rectangular opening. Two protuberances on each base of the upper labium. Papillae absent, jaw sheath and keratodonts absent.
Coloration in preservative: Predominantly pale-brownish. Light pale brown melanophoric pigment covers the dorsum. Dark brown patches scattered irregularly on the skin and condensed to form dark patches especially above the neurocranium and the whole dorsum. Laterally, jugal area and flank covered by light brown condensed reticulations mainly between the eye and the spiracle and leaving an obvious transparent spiracle on the pale body wall. Tail musculature overlaid by dense light brown reticulations leaving the lateral line conspicuous all along the tail. Fins pale and unpigmented. Ventrally, oral disk, gular and branchial regions beige with a few blotches; venter covered by light brown condensed reticulations, no intestinal coils visible.
Variation: All 19 non DNA voucher specimens of this series show the same external morphology as the voucher specimen.

Gephyromantis sculpturatus (Ahl 1929)

The following description refers to one tadpole in developmental stage Gosner 39 (Field number ZCMV 4833 - ZSM 16/2008, BL 6 mm, TL 18 mm) collected by R.D. Randrianiaina, A. Strauß, E. Reeve, J. Glos, S..Ndriantsoa, and T. Rasolonjatovo H. on 11 February 2007 in Ranomafana National Park at Piste X 175 site (21°15.846' S 47°25.161' E, 966 m a. s. l.). The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of a *G. sculpturatus* adult specimen (accession AY848432) from the same locality.
In dorsal view, body elliptical, maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 50% of BL). In lateral view, body depressed (BW 138% of BH), broadly rounded snout. Maximal body height attained between the proximal 3/5 and 4/5 of the body (SBH 63% of BL), pointed snout. Large eye (ED 19% of BL), visible from ventral view, positioned high (EH 64% of BH) laterally and directed laterally, situated between the proximal 2/10 and 3/10 of the body (SE 24% of BL), wide distance between eyes (IOD 74% of BW). Small rounded nares (ND 1.7% of BL), countersunk, positioned moderately high (NH 41% of BH) laterally and oriented ventrally, situated nearer to snout than to eye (RN 34% of NP) and lower than the eye (NH 63% of EH), moderately wide distance between nares (IND 47% of IOD), dark spot on the back of the nares absent, ornamentation absent. Small sinistral spiracle (SL 8% of BL), directed posterodorsally, visible neither from ventral nor from dorsal view and perceptible laterally; inner wall absent, rounded opening, situated between the proximal 3/5 and 4/5 of the body (SS 63% of BL), located low on the body (SH 36% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 56% of HAB). Moderately long medial vent tube (VL 11% of BL), not attached to the ventral fin. No glands. Very long tail (TAL 303% of BL), maximal tail height higher than body height (MTH 106% of BH), tail height at midtail almost equal to body height and as high as maximal tail height (THM 105% of BH and THM 100% of MTH), tail height at the beginning of the tail lower than body height (TH 80% of BH). Caudal musculature well-developed (TMW 53% of BW, TMH 70% of BH, TMH 88% of TH and 66% of MTH, TMHM 66% of THM, TMHM 66% of MTH). Tail muscle reaches tail tip. Very low fin (DF 20% of TMHM, VF 32% of MTHM), dorsal fin lower than ventral fin at mid-tail (DF 61% of VF). Dorsal fin originates on the proximal 1/4 of the tail, increases progressively to attain its maximal height at the maximal tail height and then descents slightly towards the tail tip. Ventral fin originates on the caudal musculature just behind the vent tube, ascends gradually to attain its maximal height at the maximal tail height and then declines towards the tail tip. Maximal tail height located at the 3/5 of the tail (DMTH 60% of TAL), caudal vein and myosepta not visible, point of contact axis of the tail myotomes with the body located high (HAB 65% of BH), axis of the tail myotomes not parallel with the axis of the trunk. Tail tip narrowly rounded. Very small mouth opening (ODW 8% of BW), positioned and directed ventrally. Mouth opening elliptical. Four small papillae, two each ventrolaterally of the oral disk opening. The inner papillae are larger (0.05 mm) than the outer papillae (0.3 mm). Jaw sheath and keratodonts absent.
Coloration in life (Figure 1A): Typically yellowish. Dorsal skin covered by brown varigated melanophores and some silver irridophoric spots or patches. Dorsolaterally and laterally with the same pattern as dorsally. Non pigmented spiracle perceptible. Tail musculature yellowish with irregular brown blotches that are grouped to form irregular patches, their density increases towards the tail tip; sporadic silver iridopohoric blotches present. Fins transparent, dorsal fin with many dark patches, ventral fin unpigmented. Ventrally covered by silver iridopohoric blotches mainly on the venter, oral disk and gular region transparent; branchial area reddish and beating heart visible; venter yellow with some brown and iridophoric blotches on the skin, intestinal coils invisible.
Coloration in preservative: Largely brownish. Light pale brown melanophoric pigment covers the dorsum. Dark brown patches scattered irregularly on the skin and condensed to form dark patches especially above the neurocranium and the vertebral region. Laterally, jugal area and flank with sporadic light brown blotches leaving a noticeable pale transparent spiracle on the pale body wall. Tail musculature overlaid by scattered light brown reticulations. Fins pale and provided by reticulation mainly close to the tail tip. Ventrally, oral disk, gular and branchial regions pale; venter covered by light brown reticulations, no intestinal coils visible.

Gephyromantis tschenki (Glaw & Vences 2001)

The following description refers to one tadpole in developmental stage Gosner 35, Del Pino and Escobar 23-25 (Field number ZCMV 4335 - ZSM 142/2007, BL 4.6 mm, TL 16.7 mm) collected by R.D. Randrianiaina, A. Strauß, E. Reeve, J. Glos, S..Ndriantsoa, and T. Rasolonjatovo H. on 25 February 2007 in Ranomafana National Park at Bibiango site (21°15.442' S 47°25.096' E, 962 m a. s. l.). The 16S rDNA sequence of this specimen was 98.5% identical to a reference sequence of G. *tschenki* adult specimen (accession AY848374) from the same locality.
In dorsal view, body elliptical, maximal body width attained between the proximal 3/5 and 4/5 of the body (SBW 64% of BL), broadly rounded snout. In lateral view, body depressed (BW 117% of BH), maximal body height attained at 3/5 of the body (SBH 60% of BL), pointed snout. Large eye (ED 17% of BL), visible from ventral view, positioned high (EH 63% of BH) laterally and directed laterally, situated between the proximal 1/10 and 2/10 of the body (SE 19% of BL), wide distance between eyes (IOD 62% of BW). Small rounded nares (ND 2% of BL), countersunk, positioned moderately high (NH 41% of BH) laterally and oriented ventrally, situated nearer to snout than to eye (RN 55% of NP) and lower than the eye (NH 65% of EH), wide distance between nares (IND 65% of IOD), dark spot on the back of the nares absent, ornamentation absent. Small sinistral spiracle (SL 9% of BL), directed posterodorsally, visible in ventral view and perceptible lateral view; inner wall absent, elliptical opening, situated between the proximal 2/5 and 3/5 of the body (SS 50% of BL), located low on the body (SH 38% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 64% of HAB). Long medial vent tube (VL 18% of BL), not attached to the ventral fin. No glands. Very long tail (TAL 303% of BL), maximal tail height as high as body height (MTH 100% of BH), tail height at midtail lower than body height and maximal tail height (THM 87% of BH and THM 88% of MTH), tail height at the beginning of the tail lower than body height (TH 73% of BH). Caudal musculature well-developed (TMW 47% of BW, TMH 60% of BH, TMH 81% of TH and 60% of MTH, TMHM 68% of THM, TMHM 60% of MTH). Tail muscle reaches tail tip. Very low fin (DF 25% of TMHM, VF 22% of MTHM), dorsal fin higher than ventral fin at mid-tail (DF 114% of VF). Dorsal fin originates after the dorsal body-tail junction, increases progressively to attain its maximal height at the maximal tail height and then descents slightly towards the tail tip. Ventral fin originates on the caudal musculature just behind the vent tube, ascends gradually to attain its maximal height at the maximal tail height and then declines towards the tail tip. Maximal tail height located between the proximal 3/5 and 4/5 of the tail (DMTH 69% of TAL), caudal vein visible on the proximal ¾ of the tail, myosepta invisible, point of contact axis of the tail myotomes with the body located high (HAB 60% of BH), axis of the tail myotomes not parallel with the axis of the trunk. Tail tip narrowly rounded. Very small oral disk (ODW 15% of BW), positioned and directed ventrally, not visible from dorsal view and not connected to the snout. Oral disk opening triangular, lower labium absent and upper labium folded to form a rectangular opening. Papillae absent, jaw sheath, and keratodonts absent.
Coloration in life (Figure 1B): Typically yellowish. Dorsal skin covered with brown non uniform melanophores. Dorsolaterally and laterally with the same pattern as dorsally. Rather non pigmented spiracle perceptible. Tail musculature yellowish with irregular brown blotches that group to form an irregular network, its density increases towards the tail tip. Fins yellow, with reticulations. Ventrally oral disk and gular region pale with brown blotches; branchial area reddish and beating heart visible; venter yellow, intestinal coils not visible.
Coloration in preservative: Largely brownish. Brown melanophoric pigment covers the dorsum. Dark brown patches are scattered irregularly across the skin and condense to form larger dark patches especially above the neurocranium and the vertebral and abdominal regions. Laterally, jugal area and flank with sporadic light brown blotches that condense to form reticulations; spiracle difficult to notice. Tail musculature overlaid by scattered light brown reticulations leaving the lateral line perceptible along the tail. Fins pale and provided by reticulations, mainly close to the tail tip. Ventrally, oral disk, gular and branchial regions pale with sporadic brown reticulations; venter pale, no intestinal coils visible.

Gephyromantis ventrimaculatus (Angel 1935)

The following description refers to one tadpole in developmental stage Gosner 39 (Field number ZCMV 4927 - ZSM 852/2007, BL 6.4 mm, TL 20.4 mm) collected by R.D. Randrianiaina, A. Strauß, E. Reeve, J. Glos, S..Ndriantsoa, and T. Rasolonjatovo H. on 02 March 2007 in Ranomafana National Park at Sahateza site (21°15.453' S 47°21.609' E, 1164 m a. s. l.). The 16S rDNA sequence of this specimen was 100% identical to a reference sequence of G. *ventrimaculatus* adult specimen (accession FJ559200) from Ranomafana (Ranomafanakely).
In dorsal view, body elliptical, maximal body width attained between the proximal 2/5 and 3/5 of the body (SBW 45% of BL), broadly rounded snout. In lateral view, body depressed (BW 117% of BH), maximal body height attained between the proximal 2/5 and 3/5 of the body (SBH 65% of BL), rounded snout. Large eye (ED 16% of BL), visible from ventral view, positioned moderately high (EH 59% of BH) laterally and directed laterally, situated between the proximal 2/10 and 3/10 of the body (SE 23% of BL), wide distance between eyes (IOD 76% of BW). Small round nares (ND 1.7% of BL), countersunk, positioned moderately high (NH 45% of BH) laterally and oriented ventrally, situated nearer to snout than to eye (RN 86% of NP) and lower than the eye (NH 75% of EH), moderately wide distance between nares (IND 48% of IOD), dark spot on the back of the nares absent, ornamentation absent. Small sinistral spiracle (SL 6% of BL), directed dorsally, visible from ventral and lateral views; inner wall free from body and its aperture opens posteriorly, ovoid opening, situated between the proximal 2/5 and 3/5 of the body (SS 54% of BL), located low on the body (SH 32% of BH) and below the height of the point where the axis of the tail myotomes contacts the body (SH 54% of HAB). Short medial vent tube (VL 10% of BL), not attached to the ventral fin. No glands. Very long tail (TAL 316% of BL), maximal tail height as high as body height (MTH 97% of BH), tail height at midtail almost equal to body height and maximal tail height (THM 96% of BH and THM 98% of MTH), tail height at the beginning of the tail lower than body height (TH 62% of BH). Caudal musculature well-developed (TMW 54% of BW, TMH 59% of BH, TMH 94% of TH and 60% of MTH, TMHM 72% of THM, TMHM 71% of MTH). Tail muscle reaches tail tip. Very low fin

(DF 18% of TMHM, VF 20% of MTHM), dorsal fin lower than ventral fin at mid-tail (DF 86% of VF). Dorsal fin originates on the dorsal body-tail junction, rises progressively to attain its maximal height at the maximal tail height and then descents slightly towards the tail tip. Ventral fin originates on the caudal musculature just behind the ventral terminus of the body, increases gradually to attain its maximal height at the maximal tail height and then declines towards the tail tip. Maximal tail height located between the proximal 3/5 and 4/5 of the tail (DMTH 64% of TAL), caudal vein and myosepta visible all along the tail, point of contact axis of the tail myotomes with the body located high (HAB 59% of BH), axis of the tail myotomes not parallel with the axis of the trunk. Tail tip narrowly rounded. Very small oral disk (ODW 19% of BW), positioned and directed ventrally. Oral disk opening elliptical. Papillae, jaw sheath and keratodonts absent.
Coloration in life (Figure 1C): Typically black, covered by scattered silver iridophoric pigments.
Coloration in preservative: Largely black, the area occupied by the iridophoric pigment gives light pattern. Spiracle perceivable, intestine not visible.

Appendix 2

Summary of localities with geographic coordinates, and collection dates

Table 1. Summary of localities with geographic coordinates, and collection dates of *Boophis* tadpoles

Locality	Site	Species	Coordinates	Date	Collectors
Ankijagna Lalagna		*B. sambirano* [Ca49]	14.23425°S 48.97887°E 1187m a.s.l.	08.06.2010	D.R. Vieites, F.M. Ratsoavina, A.S. Rasamison, A . Rakotoarisoa, M. Vences, R.D. Randrianiaina
Ambohitsara		*B. albipunctatus*	21°21.431' S 47°48.941' E 294 m a.s.l.	03.03.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
Ambinanitelo		*B. marojezensis* [Ca52]	14.22540°S 48.96346°E 1182m a.s.l.	09.06.2010	D.R. Vieites, F.M. Ratsoavina, A.S. Rasamison, A . Rakotoarisoa, M. Vences, R.D. Randrianiaina
Ambinanitelo		*B. sambirano* [Ca50]	14.22540°S 48.96346°E 1182m a.s.l.	09.06.2010	D.R. Vieites, F.M. Ratsoavina, A.S. Rasamison, A . Rakotoarisoa, M. Vences, R.D. Randrianiaina
An'Ala	Andohanisity	*B. mandraka* [Ca46]	18.91926°S 48.48796°E 889 m a.s.l.	08.02.2006	C. Patton, D.R. Vieites, J. Patton, L. Raharivololoniaina, M. Vences, R.D. Randrianiaina
Andasibe Special Reserve	Analamazaotra river	*B. sibilans*	18°55'54''S 48°25'44''E 900m a.s.l.	04.12.2001	L. Raharivololoniaina, M. Vences
Between Antsohihy and Bealanana	Anjingo river	*B. sambirano* [Ca47]	14°44'55.7"S 48°29'29.4"E 925m a.s.l.	07.06.2010	D.R. Vieites, F.M. Ratsoavina, A.S. Rasamison, A . Rakotoarisoa, M. Vences, R.D. Randrianiaina
Between Antsohihy and Bealanana	Anjingo river	*B. sambirano* [Ca48]	14°44'55.7"S 48°29'29.4"E 925m a.s.l.	07.06.2010	F.M. Ratsoavina, A.S. Rasamison, A . Rakotoarisoa, D.R. Vieites, M. Vences, R.D. Randrianiaina
Manongarivo Special Reserve	Camp Norbert	*B. sambirano*	13°56.053' S 48°27.028''E 288 m a.s.l.	31.01.2003	F. Glaw, M. Vences, R.D. Randrianiaina
Marojejy National Park	Camp Mantella	*B. vittatus*	14°26.972' S 49°47.214' E 327 m a.s.l.	14.02.2005	F. Glaw, M. Vences, R.D. Randrianiaina
Marojejy National Park	Camp Marojejia	*B. englaenderi*	14°26.070' S 49°45.638' E 740 m a.s.l.	18.02.2005	F. Glaw, M. Vences, R.D. Randrianiaina
Marojejy National Park	Camp Mantella	*B. englaenderi* [Ca45]	14°26.972' S 49°47.214' E 327 m a.s.l.	19.02.2005	F. Glaw, M. Vences, R.D. Randrianiaina
Marojejy National Park	Camp Mantella	*B. marojezensis* [Ca25]	14°26.972' S 49°47.214' E 327 m a.s.l.	19.02.2005	F. Glaw, M. Vences, R.D. Randrianiaina
Marojejy National Park	Camp Mantella	*B. marojezensis* [Ca26]	14°26.972' S 49°47.214' E 327 m a.s.l.	19.02.2005	F. Glaw, M. Vences, R.D. Randrianiaina
Marojejy National Park	Camp Mantella	*B. sibilans*	14°26.972' S 49°47.214' E 327 m a.s.l.	19.02.2005	F. Glaw, M. Vences, R.D. Randrianiaina
Ranomafana National Park	Ambatolahy river	*B. andohahela*	21°14'897"S 47°25'769"E 867m a. s. l.	27.07.2009	R.D. Randrianiaina
Ranomafana National Park	Ambatolahy river	*B. marojezensis* [Ca51]	21°14'897"S 47°25'769"E 867m a.s.l.	27.07.2009	R.D. Randrianiaina
Ranomafana National Park	Ambatolahy river	*B. schuboeae*	21°14'897"S 47°25'769"E 867m a.s.l.	27.07.2009	R.D. Randrianiaina
Ranomafana National Park	Imaloka	*B. marojezensis* [Ca51]	21.24215°S 47.46563°E 957m	01.03.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
Ranomafana National Park	In a pool below waterfall	*B. schuboeae*		11.02.2003	M. Teschke, M. Vences
Ranomafana National Park	Marihy avaratra	*B. luciae*	21.62448°S 47.41944°E 1144m a.s.l.	20.02.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
Ranomafana	Marihy avaratra	*B. mandraka* [Ca38]	21°47.469 S	02.02.2007	A. Strauß, J. Glos, E. Reeve,

National Park			47°25.166 E 955m		T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
Ranomafana National Park	Talatakely	*B. luciae*	21°15.846' S 47°25.161' E 966 m a.s.l.	24.02.2006	L. Rahariviololoniaina, A.F. Ranjanaharisoa, T.J. Razafindrabe, D.R. Vieites, J. Patton, C. Patton, M. Vences, R.D. Randrianiaina
Ranomafana National Park	Talatakely	*B. marojezensis* [Ca51]	21°15.846' S 47°25.161' E 966 m a.s.l.	24.02.2006	L. Rahariviololoniaina, A.F. Ranjanaharisoa, T.J. Razafindrabe, D.R. Vieites, J. Patton, C. Patton, M. Vences, R.D. Randrianiaina
Ranomafana National Park	Sahateza (Pond Donald)	*B. ankaratra*	21.25793°S 047.35972°E 1164m	03.03.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
Ranomafana National Park	Vatoharana	*B. andohahela*	21.28897°S 047.42942°E 1016m	24.03.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
Tsaratanana Integral National Reserve	Antevialambazaha	*B. marojezensis* [Ca53]	14.17425°S 048.94524°E 1699m	10.06.2010	D.R. Vieites, F.M. Ratsoavina, A.S. Rasamison, A . Rakotoarisoa, M. Vences, R.D. Randrianiaina

Table 2. Summary of localities with geographic coordinates, and collection dates of *Boophis picturatus* and *B. majori* tadpoles

Species	Locality	Fieldnumber	ZSM	Coordinates	Date	Collectors
B. picturatus	Ambohitsara	ZCMV 4941	77/2008	21°21.431' S 47°48.941' E 294 m a.s.l.	03.03.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
B. picturatus	An'Ala	ZCMV 3406	1711/2007	18°55.156' S 48°29.277' E 889 m a.s.l.	08.02.2006	C. Patton, D.R. Vieites, J. Patton, L. Raharivololoniaina, M. Vences, R.D. Randrianiaina
B. picturatus	An'Ala	ZCMV 3487	1791/2007	18°55.156' S 48°29.277' E 889 m a.s.l.	08.02.2006	C. Patton, D.R. Vieites, J. Patton, L. Raharivololoniaina, M. Vences, R.D. Randrianiaina
B. picturatus	Belle Vue (RNP)	ZCMV 5189	608/2007	21°15.582' S 47°25.320' E 963 m a.s.l.	12.03.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
B. picturatus	Bibiango (RNP)	ZCMV 4329	172/2007	21°15.442' S 47°25.096' E 930 m a.s.l.	25.02.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
B. picturatus	Fierenana	FG/MV 2002.1664	808/2004	18°32'36"S 48°26'56"E 948 m s.s.l.	2002	M. Teschke, M. Vences
B. picturatus	Fierenana	FG/MV 2002.1664	839/2004	18°32'36"S 48°26'56"E 948 m s.s.l.	2002	M. Teschke, M. Vences
B. picturatus	Fompohonina II (RNP)	ZCMV 4017	680/2007	21°16.088' S 47°25.423' E 996 m a.s.l.	15.03.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
B. picturatus	Fompohonina IV (RNP)	T 08/0076	-	21°16.115' S 47°25.520' E 990 m a.s.l.	10.07.2008	R.D. Randrianiaina
B. picturatus	Vevembe	-	833/2004	22°47.686' S 47°11.228' E 581 m a.s.l.	10.02.2004	M. Teschke, M. Vences
B. picturatus	Ranomena (RNP)	ZCMV 3807	172/2008	21°12,1'S 47°27,4'E 970 m a.s.l.	28.02.2006	L. Raharivololoniaina, A.F. Ranjanaharisoa, T.J. Razafindrabe, D.R. Vieites, J. Patton, C. Patton, M. Vences, R.D. Randrianiaina
B. picturatus	Sahamalaotra (RNP)	FG/MV 2002.1835	821/2004	21°14.112' S 47°23.767' E 1124 m a.s.l.	2002	M. Teschke, M. Vences
B. picturatus	Sahamalaotra (RNP)	ZCMV 5050	196/2007	21°14.112' S 47°23.767' E 1124 m a.s.l.	06.03.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
B. majori	Ankidoanavo (RNP)	ZCMV 1369	37/2007	21.22562° S 43.37028° E 1144 m a.s.l.	19.02.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
B. majori	Ranomena (RNP)	ZCMV 5398	953/2007	21°12,1' S 47°27,4' E 970 m a.s.l.	19.03.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
B. majori	Vohiparara	ZCMV 2641	397/2008	21°14.143' S 47°23.152' E 1118 m a.s.l	24.02.2006	L. Raharivololoniaina, A.F. Ranjanaharisoa, T.J. Razafindrabe, D.R. Vieites, J. Patton, C. Patton, M. Vences, R.D. Randrianiaina

Table 3. Summary of localities with geographic coordinates, and collection dates of *Ochthomantis* tadpoles

Locality	Site	Species	Coordinates	Date	Collectors
Ambohitsara		*M. mocquardi*	21°21.431' S 47°48.941' E 294 m a.s.l.	03.03.2007	A. Strauß, J. Glos, E. Reeve, T. Rasolonjatovo- H., S. Ndriantsoa, M. Vences, R.D. Randrianiaina
An'Ala	Andohanisity	*M. argenteus*	18°55.156' S 48°29.277' E 889 m a.s.l.	08.02.2006	C. Patton, D.R. Vieites, J. Patton, L. Raharivololoniaina, M. Vences, R.D. Randrianiaina
		M. femoralis			
		M. mocquardi			
		M. zolitschka			
Isalo National Park	South of Tevan'ny mpiolitsa	*M. femoralis*	22°30.085' S 45°17.177' E 869 m a.s.l.	04.04.2007	S. Ndriantsoa, R.D. Randrianiaina
Mahasoa		*M. mocquardi*	17°17.861' S 48°42.119' E 1032 m a.s.l.	13.02.2006	D.R. Vieites, P. Bora, J. Patton, C. Patton, M. Vences
Marojejy National Park	Camp Mantella	*M. femoralis*	14°26.972' S 49°47.214' E 327 m a.s.l.	19.02.2003	F. Glaw, M. Vences, R.D. Randrianiaina
		M. sp. 43			
Montagne d'Ambre National Park	Voie des milles arbres	*M. ambreensis*	12°31.616' S 49°10.316' E 1050 m a.s.l.	17.02.2003	F. Glaw, M. Vences, R.D. Randrianiaina
		M. sp. 42			
Ranomafana	Sahamalaotra	*M. majori*	21°14.112' S 47°23.767' E 1124 m a.s.l.	25.02.2006	L. Raharivololoniaina, A.F. Ranjanaharisoa, T.J. Razafindrabe, D.R. Vieites, J. Patton, C. Patton, M. Vences, R.D. Randrianiaina
	Imaloka	M. sp. 47	21°15.846' S 47°25.161' E 966 m a.s.l.	24.02.2006	
	Maharira	M. sp. 47	21°19.547' S 47°24.147' E 1200 m a.s.l.	26.01.2004	I. De la Riva, M. Vences
	Vohiparara	*M. femoralis*	21°14.143' S 47°23.152' E 1118 m a.s.l.	20.02.2006	L. Raharivololoniaina, A.F. Ranjanaharisoa, T.J. Razafindrabe, D.R. Vieites, J. Patton, C. Patton, M. Vences, R.D. Randrianiaina
	Ranomafana village	M. sp. 64	21°15.699' S 47°27.571' E 619 m a.s.l.	21.02.2006	L. Raharivololoniaina, A.F. Ranjanaharisoa, T.J. Razafindrabe, D.R. Vieites, J. Patton, C. Patton, M. Vences, R.D. Randrianiaina
Vevembe forest		*M. femoralis*	22°47.686' S 47°11.228' E 581 m a.s.l.	10.02.2004	M. Vences
		M. majori			

Appendix 3

Measurements data

Table 1. Morphometric measurements (all in mm) of all strongly rheophilus *Boophis* DNA voucher specimens. For abbreviations, see Materials and Methods

Species	*Boophis englaenderi*	*Boophis englaenderi* [Ca45]	*Boophis andohahela*	*Boophis ankaratra*	*Boophis schuboeae*	*Boophis albipunctatus*	*Boophis sibilans*	*Boophis luciae*	*Boophis sambirano*	*Boophis ämandraka* [Ca38]	*Boophis mandraka* [Ca46]	*Boophis Sambirano* [Ca47]	*Boophis sambirano* [Ca48]	*Boophis sambirano* [Ca49]	*Boophis sambirano* [Ca50]	*Boophis marojezensis*	*Boophis marojezensis* [Ca25]	*Boophis marojezensis* [Ca26]	*Boophis marojezensis* [Ca51]	*Boophis marojezensis* [Ca52]	*Boophis marojezensis* [Ca53]	*Boophis vittatus*
Field number	FGZC 2244	FGZC 2957	T 428	ZCMV 4917	FGMV 2003-1800	ZCMV 4946	FGZC 2956	ZCMV 5146	FGMV 2003-1902	ZCMV 4261	ZCMV 3479	ZCMV 13105	ZCMV 13109	ZCMV 13155	ZCMV 13172	FGZC 2277	FGZC 2929	FGZC 2930	ZCMV 3691	ZCMV 13168	ZCMV 13200	FGZC 2238
ZSM number	623/2008	1632/2007	998/2007	876/2007	978/2004	82/2008	1631/2007	730/2007	672/2004	456/2007	1784/2007	482/2010	485/2010	528/2010	545/2010	1528/2007	1611/2007	1612/2007	267/2008	541/2010	573/2010	1906/2007
Date of capture	14.02.2005	19.02.2005	24.03.2007	02.03.2007	22.01.2003	03.03.2007	19.02.2005	08.03.2007	31.01.2003	20.02.2007	08.02.2006	07.06.2010	07.06.2010	08.06.2010	09.06.2010	16.02.2005	19.02.2005	19.02.2005	24.02.2006	09.06.2010	10.06.2010	14.02.2005
Site	Marojejy	Marojejy	Ranomafana	Ranomafana	Ranomafana	Ranomafana	Marojejy	Ranomafana	Manongarivo	Ranomafana	An'Ala	Anjingo river	Anjingo river	Ankijagna Lagnana	Ambinanitelo	Marojejy	Marojejy	Marojejy	Ranomafana	Ambinanitelo	Tsaratanana	Marojejy
Stage	36	30	26	28	36	25	29	36	27	26	25	27	27	27	27	27	29	29	29	28	27	25
BL	11.8	10.5	11.0	11.3	12.1	7.5	11.0	10.4	8.2	7.6	6.8	13.5	12.7	11.7	11.7	7.6	7.8	8.8	8.9	10.5	9.6	5.9
BW	6.4	5.5	5.0	6.7	6.8	3.9	5.7	4.8	5.2	4.7	3.5	7.9	6.9	7.7	7.0	4.5	4.7	4.9	5.0	6.2	5.8	3.2
SBW	5.1	7.0	6.1	8.4	5.8	5.0	5.3	4.0	4.6	4.3	3.6	6.8	6.1	8.2	7.7	4.2	5.4	4.8	4.6	6.9	5.4	3.0
BH	4.8	4.6	4.3	5.2	4.7	2.8	4.6	3.4	3.9	3.6	2.9	5.2	4.7	6.0	5.5	3.8	4.0	4.5	4.7	5.2	4.2	2.6
SBH	8.7	7.5	8.2	8.7	8.1	5.9	8.2	5.2	6.6	4.9	4.6	10.0	8.4	8.4	8.6	5.1	5.4	5.1	6.1	7.4	6.8	4.2
ED	1.9	1.5	1.5	1.8	1.8	0.9	1.4	1.7	1.1	1.1	1.0	1.9	1.6	1.6	1.6	1.1	1.1	1.3	1.6	1.7	1.3	0.9
SE	4.4	4.1	3.5	4.3	4.2	3.3	4.7	4.0	4.0	3.7	3.3	6.4	5.7	4.5	5.3	3.3	3.2	3.5	3.1	4.3	4.5	2.6
EH	4.1	3.6	3.0	4.1	3.5	2.2	3.6	2.4	3.3	2.8	2.2	4.3	3.9	4.3	4.3	3.0	3.0	3.1	3.7	3.8	3.2	1.8
IOD	4.7	3.8	4.1	4.1	4.4	2.6	4.2	3.7	3.2	2.8	2.5	4.3	4.6	4.2	3.9	3.0	3.2	3.6	4.3	4.5	3.9	2.7
ND	0.6	0.3	0.3	0.3	0.3	0.2	0.3	0.3	0,2	0.2	0.2	0.8	0.4	0.6	0.5	0.2	0.3	0.3	0.3	0.3	0.3	0.2
NH	4.0	3.4	2.4	3.5	3.0	2.3	3.6	2.3	3.3	2.8	2.4	4.7	4.2	4.2	4.5	2.8	2.9	2.8	3.4	3.6	2.9	1.8
IND	2.1	1.9	2.1	2.2	2.1	1.4	1.9	1.9	1.5	1.7	1.3	2.2	2.0	2.0	2.3	1.6	1.7	1.8	1.9	2.1	2.0	1.2
RN	1.9	2.0	1.3	2.2	2.2	1.8	2.4	2.0	2.4	2.1	2.2	4.0	3.6	2.3	3.1	1.7	1.6	1.6	1.4	2.0	2.2	1.3
NP	2.5	2.1	2.2	2.1	2.1	1.5	2.3	1.9	1.5	1.7	1.1	2.4	2.2	2.2	2.3	1.6	1.6	1.9	1.8	2.2	2.3	1.3
SL	1.4	1.6	1.5	2.1	2.3	1.2	2.2	1.3	1.4	1.3	0.9	2.7	1.7	1.9	1.6	1.4	1.5	1.5	1.8	1.8	1.5	0.9
SS	7.5	7.0	6.7	8.4	9.0	5.5	8.3	6.8	6.8	6.4	4.9	10.9	9.4	9.0	9.3	5.7	5.8	6.6	5.8	7.5	7.8	4.5
SV	4.3	3.4	4.3	3.0	3.0	1.9	2.7	3.6	1.3	1.3	1.9	2.7	3.3	2.7	2.4	2.0	1.9	2.2	3.1	3.0	1.9	1.4
SH	1.7	1.5	1.8	1.6	1.9	1.2	2.0	0.6	1.4	0.9	1.0	1.8	1.7	1.7	1.9	2.0	1.4	1.5	1.7	1.8	1.8	0.8
VL	1.1	1.0	1.3	1.2	1.0	0.9	1.2	1.5	0.6	0.6	0.5	1.2	1.1	1.2	0.9	0.6	1.9	1.0	0.9	1.1	1.2	0.3
TAL	18.2	19.1	20.1	18.7	19.7	11.6	20.2	17.4	12.7	11.1	10.8	19.2	17.9	19.0	17.7	13.9	13.8	15.7	14.9	19.8	17.5	11.2
TMW	3.5	3.6	3.2	3.5	3.7	2.0	3.4	2.6	2.2	1.8	1.8	4.1	3.4	3.5	3.6	2.3	2.7	2.8	3.4	3.7	3.0	1.9
TMH	3.7	3.7	3.1	3.5	3.3	1.9	3.5	2.9	2.5	1.9	1.7	3.7	3.6	3.6	3.6	2.5	2.5	2.8	3.3	3.7	2.7	2.1
TH	4.2	3.7	3.7	4.4	3.3	2.4	4.2	2.9	2.6	2.8	2.4	3.7	3.6	3.6	3.6	3.0	3.5	3.8	3.8	4.2	3.3	2.5
TMHM	2.6	2.9	2.9	2.4	2.6	1.3	2.6	2.2	1.6	1.3	1.6	2.6	2.4	2.7	2.5	1.7	2.1	2.2	2.7	2.8	2.2	1.6
THM	3.9	4.6	4.3	4.5	4.4	2.9	5.3	3.7	2.6	2.9	3.1	4.6	4.5	5.0	5.0	3.5	3.8	4.3	3.9	5.4	4.6	2.7

MTH	4.3	4.6	4.4	4.7	4.4	3.1	5.3	3.7	2.6	3.2	3.1	4.6	4.5	5.0	5.0	3.7	3.8	4.3	4.0	5.5	4.8	2.7
DMTH	8.0	11.8	9.2	4.5	9.9	3.9	10.2	7.9	5.5	4.3	5.4	9.6	8.9	9.5	8.8	6.0	6.4	7.7	8.5	8.9	7.6	4.3
DF	0.9	1.2	0.9	1.1	1.2	0.9	1.5	0.8	0.5	1.1	0.9	1.6	1.4	1.5	1.6	1.1	1.1	1.3	0.8	1.6	1.6	0.6
VF	0.5	0.6	0.6	1.0	0.6	0.7	1.2	0.7	0.4	0.5	0.6	0.5	0.7	0.8	0.8	0.7	0.7	0.8	0.4	1.0	0.9	0.5
HAB	3.2	2.6	2.3	3.1	3.0	1.6	2.5	1.8	2.2	1.9	1.7	3.3	2.7	3.7	3.0	2.4	2.4	2.8	2.9	2.9	2.5	1.5
TL	29.9	29.5	31.2	30.1	31.8	19.1	31.2	27.8	17.8	18.8	17.6	32.8	30.6	30.7	29.3	18.3	21.6	24.4	23.8	30.3	27.1	17.1

Table 2. Relative value (all in percentage) of all the morphometric parameters of all strongly rheophilus *Boophis* DNA voucher specimens. For abbreviations, see Materials and Methods.

Species	*Boophis englaenderi*	*Boophis englaenderi* [Ca45]	*Boophis andohahela*	*Boophis ankaratra*	*Boophis schuboeae*	*Boophis albipunctatus*	*Boophis sibilans*	*Boophis luciae*	*Boophis sambirano*	*Boophis mandraka* [Ca38]	*Boophis mandraka* [Ca46]	*Boophis sambirano* [Ca47]	*Boophis sambirano* [Ca48]	*Boophis sambirano* [Ca49]	*Boophis sambirano* [Ca50]	*Boophis marojezensis*	*Boophis marojezensis* [Ca25]	*Boophis marojezensis* [Ca26]	*Boophis marojezensis* [Ca51]	*Boophis marojezensis* [Ca52]	*Boophis marojezensis* [Ca53]	*Boophis vittatus*
Field number	FGZC 2244	FGZC 2957	T 428	ZCMV 4917	FGMV 2003-1800	ZCMV 4946	FGZC 2956	ZCMV 5146	FGMV 2003-1902	ZCMV 4261	ZCMV 3479	ZCMV 13105	ZCMV 13109	ZCMV 13155	ZCMV 13172	FGZC 2277	FGZC 2929	FGZC 2930	ZCMV 3691	ZCMV 13168	ZCMV 13200	FGZC 2238
ZSM number	623/2008	1632/2007	998/2007	876/2007	978/2004	82/2008	1631/2007	730/2007	672/2004	456/2007	1784/2007	482/2010	485/2010	528/2010	545/2010	1528/2007	1611/2007	1612/2007	267/2008	541/2010	573/2010	1906/2007
Date of capture	14.02.2005	19.02.2005	24.03.2007	02.03.2007	22.01.2003	03.03.2007	19.02.2005	08.03.2007	31.01.2003	20.02.2007	08.02.2006	07.06.2010	07.06.2010	08.06.2010	09.06.2010	16.02.2005	19.02.2005	19.02.2005	24.02.2006	09.06.2010	10.06.2010	14.02.2005
Site	Marojejy	Marojejy	Ranomafana	Ranomafana	Ranomafana	Ranomafana	Marojejy	Ranomafana	Manongarivo	Ranomafana	An'Ala	Anjingo river	Anjingo river	Ankijagna Lagnana	Ambinanitelo	Marojejy	Marojejy	Marojejy	Ranomafana	Ambinanitelo	Tsaratanana	Marojejy
Stage	36	30	26	28	36	25	29	36	27	26	25	27	27	27	27	27	29	29	29	28	27	25
BW/BL	54	52	45	59	57	52	52	46	63	61	52	58	54	66	60	58	61	56	55	59	60	53
SBW/BL	44	66	55	74	48	67	48	38	57	56	53	50	48	70	66	55	70	55	51	65	56	50
BW/BH	133	120	117	129	145	139	124	141	132	131	122	153	145	128	128	117	117	110	106	119	138	120
SBH/BL	74	71	75	77	67	79	75	50	81	63	67	74	66	72	73	67	70	58	68	71	71	71
ED/BL	16	14	14	16	15	13	13	17	14	15	15	14	12	14	13	14	15	15	18	16	14	15
SE/BL	38	39	32	38	35	44	43	38	49	49	49	48	45	38	46	43	41	40	35	41	47	44
EH/BH	85	78	69	78	73	77	78	71	86	77	75	84	83	72	79	79	74	68	80	73	76	69
IOD/BW	74	69	82	60	65	68	73	79	59	59	72	55	67	55	56	67	68	73	86	72	67	85
ND/BL	4.8	2.9	2.5	2.4	2.5	2.7	2.5	2.4	3.9	3.1	3.2	6.0	3.0	4.7	3.9	3	3.5	3.3	3.4	2.8	3.1	3.5
NH/BH	83	75	57	67	64	83	78	69	84	77	85	92	89	70	82	74	71	63	72	70	70	70
RN/NP	75	92	60	106	104	120	108	105	159	125	194	166	167	107	136	109	96	85	78	92	96	103
NH/EH	97	96	82	86	87	108	100	97	98	101	112	109	108	98	103	94	97	92	90	95	92	101
IND/IOD	44	50	50	54	48	52	47	51	50	61	53	51	44	46	58	53	53	49	45	47	51	46
SL/BL	11	15	14	19	19	16	20	12	16	17	13	20	14	16	14	19	19	17	20	17	16	16
SS/BL	64	67	61	74	75	74	75	65	84	83	72	80	74	77	79	74	75	75	65	71	81	76
SH/BH	36	32	41	31	41	43	44	17	35	25	34	35	36	28	36	53	34	34	37	35	44	31
SH/HAB	54	58	76	53	64	76	83	31	62	47	59	54	63	45	65	84	57	54	60	62	74	55
VL/BL	9	9	12	11	9	12	11	15	8	8	7	9	8	11	8	8	24	12	10	10	13	4
TAL/BL	155	182	183	165	163	156	184	167	156	146	159	142	141	163	151	181	178	178	167	189	182	188
TMW/BW	54	66	63	51	54	52	59	56	43	37	52	51	50	46	51	52	57	57	68	59	53	59
TMH/BH	76	81	72	68	69	68	75	86	65	54	58	72	76	60	66	65	62	63	69	71	64	80
TMH/TH	87	100	83	81	100	80	83	100	96	70	71	100	100	100	100	81	72	74	86	88	82	86
TMH/MTH	85	81	70	76	74	62	66	79	96	61	54	80	81	72	72	66	66	65	81	68	55	79
TH/BH	88	81	86	84	69	86	91	86	67	77	82	72	76	60	66	80	87	85	80	81	78	94
TMHM/THM	66	62	67	53	59	45	50	60	63	46	52	55	53	54	51	49	55	52	69	52	47	59

TMHM/MTH	61	62	65	51	59	42	50	59	63	41	52	55	53	54	51	47	55	52	66	51	45	58
THM/BH	82	100	100	86	94	102	113	108	67	80	107	90	95	83	91	93	95	96	82	102	111	101
THM/MTH	92	100	97	96	100	93	100	98	96	90	100	100	100	100	100	95	100	100	96	98	95	99
MTH/BH	90	101	103	90	94	110	113	110	67	89	107	90	95	83	91	98	95	96	86	104	116	102
DMTH/TAL	44	62	46	24	50	34	50	45	43	38	50	50	50	50	50	43	47	49	57	45	43	39
DF/TMHM	34	41	30	46	47	72	57	37	31	83	58	61	60	56	65	61	52	57	30	56	72	38
VF/TMHM	18	19	21	43	23	52	44	32	22	36	35	18	30	29	33	42	32	36	15	36	41	32
DF/VF	189	209	144	109	200	137	130	117	154	232	166	344	201	191	198	144	163	159	193	155	176	118
HAB/BH	66	56	54	59	64	57	53	54	57	53	58	64	57	62	55	63	59	62	62	56	60	57

Table 3. Comparison of the oral disk characteristic of all strongly rheophilus *Boophis* voucher specimens described in this paper. JW, MCL, DG, $A_{1,}$ Kerat length, MP lenght and SMP length in mm. ODW/BW, DG/ODW, JW/ODW, MCL/JW and A_1/ODW in percentage. A_1 density per millimeter. For abbreviations. see Materials and Methods. **A:** upper and lower sheaths have the same size, **B:** upper sheath of smaller size. **C:** Upper sheath rudimentary, **D:** upper sheath absent; **E:** typical lower sheath (totally keratinised with smooth surface), **F:** ribbed lower sheath (composed of a series of fused columns with irregular surface); **G:** upper labium is a continuation of the snout, **H:** the entire margin is free from the snout

Species	*Boophis englaenderi*	*Boophis englaenderi* [Ca45]	*Boophis andohahela*	*Boophis ankaratra*	*Boophis schuboeae*	*Boophis albipunctatus*	*Boophis sibilans*	*Boophis luciae*	*Boophis sambirano*	*Boophis mandraka* [Ca38]	*Boophis mandraka* [Ca46]	*Boophis sambirano* [Ca47]	*Boophis sambirano* [Ca48]	*Boophis sambirano* [Ca49]	*Boophis sambirano* [Ca50]	*Boophis marojezensis*	*Boophis marojezensis* [Ca25]	*Boophis marojezensis* [Ca26]	*Boophis marojezensis* [Ca51]	*Boophis marojezensis* [Ca52]	*Boophis marojezensis* [Ca53]	*Boophis vittatus*
Field number	FGZC 2244	FGZC 2957	T 428	ZCMV 4917	FGMV 2003-1800	ZCMV 4946	FGZC 2956	ZCMV 5146	FGMV 2003-1902	ZCMV 4261	ZCMV 3479	ZCMV 13105	ZCMV 13109	ZCMV 13155	ZCMV 13172	FGZC 2277	FGZC 2929	FGZC 2930	ZCMV 3691	ZCMV 13168	ZCMV 13200	FGZC 2238
ZSM number	623/2008	1632/2007	998/2007	876/2007	978/2004	82/2008	1631/2007	730/2007	672/2004	456/2007	1784/2007	482/2010	485/2010	528/2010	545/2010	1528/2007	1611/2007	1612/2007	267/2008	541/2010	573/2010	1906/2007
Date of capture	14.02.2005	19.02.2005	24.03.2007	02.03.2007	22.01.2003	03.03.2007	19.02.2005	08.03.2007	31.01.2003	20.02.2007	08.02.2006	07.06.2010	07.06.2010	08.06.2010	09.06.2010	16.02.2005	19.02.2005	19.02.2005	24.02.2006	09.06.2010	10.06.2010	14.02.2005
Site	Marojejy	Marojejy	Ranomafana	Ranomafana	Ranomafana	Ranomafana	Marojejy	Ranomafana	Manongarivo	Ranomafana	An'Ala	Anjingo river	Anjingo river	Ankijagna Lagnana	Ambinanitelo	Marojejy	Marojejy	Marojejy	Ranomafana	Ambinanitelo	Tsaratanana	Marojejy
Stage	36	30	26	28	36	25	29	36	27	26	25	27	27	27	27	27	29	29	29	28	27	25
ODW	3.5	4.6	3.7	4.9	5.1	3.2	4.6	4.3	4.3	4.2	3.6	7.3	7.4	5.7	6.7	3,65	3.2	3.7	3.6	3.8	3.9	2.5
LTRF	6(3-6)/3(2-3)	7(3-7)/3	6(3-6)/3	8(5-8)/3	8(5-8)/3	7(5-7)/3	7(5-7)/3	7(5-7)/3	8(6-8)/3	8(6-8)/3	8(6-8)/3	8(6-8)/3	8(6-8)/3	8(6-8)/3	8(6-8)/3	7(5-7)/3	7(5-7)/3	7(5-7)/3	7(5-7)/3	7(5-7)/3	7(5-7)/3	7(5-7)/3
UR	6	7	6	8	8	7	7	7	8	8	8	8	8	8	8	7	7	7	7	7	7	7
LR	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
JW	1.63	1.42	1.32	1.65	1.68	0.96	1.46	1.42	1,56	1.34	1.12	2.42	2.33	1.88	2.14	1,17	0.96	1.17	1.26	1.24	1.36	0.93
MCL	0.04	0.04	0.11	0.17	0.11	abs	abs	abs	Abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs
DG	3.00	3.06	2.60	2.55	2.98	1.33	2.19	2.39	1.67	1.63	0.50	2.73	2.71	1.34	1.93	abs	abs	abs	abs	abs	abs	abs
VG	abs	abs	abs	abs	abs	abs	abs	abs	Abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs
$A_{1\,len}$	3.20	3.75	3.30	2.59	2.47	1.67	2.31	2.57	1.46	1.63	0.74	2.58	2.64	1.26	1.87	1,85	1.66	1.85	1.76	1.92	1.78	1.23
$A_{2\,len}$	2.97	3.83	2.15	3.20	3.21	2.38	3.33	3.33	3.36	2.60	1.92	6.43	5.01	3.39	4.56	2,82	2.42	2.82	2.63	3.04	3.54	1.57
$A_{3\,len}$ (R/L)	1.24/1.26	1.82/1.80	1.44/1.49	3.65	3.59	2.91	4.27	4.00	4.03	3.33	2.77	4.95	6.08	4.61	6.03	3,34	3.28	3.40	3.28	3.73	4.47	2.01
$A_{4\,len}$ (R/L)	0.98/0.83	1.44/1.48	1.07/1.14	3.86	3.75	3.51	4.64	4.11	4.63	4.03	3.01	7.79	6.80	5.53	5.84	3,35	3.04	3.39	3.48	3.69	4.45	2.49
$A_{5\,len}$ (R/L)	0.68/0.58	1.07/1.09	0.80/0.92	1.75/1.70	1.79/1.88	1.33/1.38	2.27/2.19	1.78/1.79	4.87	4.08	3.24	8.20	7.29	5.48	7.07	1,15/1,31	1.17/1.19	1.19/1.30	1.30/1.31	1.57/1.54	1.90/1.92	1.04/1.03
$A_{6\,len}$ (R/L)	0.45/0.37	0.68/0.73	0.57/0.60	1.35/1.27	1.37/1.47	0.99/0.99	1.65/1.64	1.29/1.37	2.20/2.25	1.79/1.92	1.54/1.48	3.9/3.62	3.41/3.48	2.56/2.31	3.4/3.5	0,76/0,91	0.82/0.89	0.81/0.85	0.94/1.02	1.12/1.18	1.36/1.35	0.73/0.65
$A_{7\,len}$ (R/L)	abs	0.46/0.30	abs	0.83/0.68	1.04/1.03	0.69/0.74	1.15/1.19	0.84/0.81	1.61/1.74	1.20/1.18	1.08/1.02	2.68/2.57	2.77/2.81	1.87/1.93	2.54/2.59	0,39/0,48	0.49/0.58	0.65/0.41	0.52/0.57	0.66/0.68	0.84/0.88	0.43/0.40
$A_{8\,len}$ (R/L)	abs	abs	abs	0.47/0.38	0.77/0.84	abs	abs	abs	0.85/0.94	0.59/0.63	0.47/0.42	1.60/1.32	1.58/1.73	1.11/1.08	1.3/1.4	abs	abs	abs	abs	abs	abs	abs
$P_{1\,len}$	2.49	3.39	2.56	3.85	4.19	2.44	3.77	3.18	4.28	3.79	2.90	6.42	6.41	4.97	6.74	2,7	2.21	2.40	2.63	3.54	3.25	1.87
$P_{2\,len}$	2.69	3.79	2.79	4.15	4.56	2.71	4.19	3.55	4.75	4.05	3.07	6.91	6.94	5.49	7.33	3,04	2.54	2.92	2.90	4.25	3.51	2.08
$P_{3\,len}$	2.64	4.18	2.95	4.44	4.90	2.69	4.70	3.82	4.22	4.13	3.11	7.42	7.13	5.60	7.57	3,30	2.80	3.45	3.24	4.62	3.84	2.06
Kerat len	0.10	0.11	0.15	0.12	0.10	0.07	0.13	0.15	0.09	0.10	0.07	0.20	0.15	0.13	0.14	0,13	0.08	0.13	0.10	0.16	0.17	0.08
MP len	0.12	0.12	0.08	0.08	0.11	0.07	0.08	0.14	0.09	0.08	0.04	0.16	0.11	0.13	0.10	0,12	0.10	0.17	0.10	0.07	0.08	0.09
SMP length	0.09	0.13	0.08	0.11	0.10	0.07	0.08	0.10	0.11	0.09	0.07	0.25	0.18	0.15	0.12	0,12	0.05	0.08	0.10	0.09	0.11	0.05
ODW/BW	56	84	75	73	74	84	80	91	95	90	101	93	108	74	95	87	68	74	72	62	68	78
ODW/BL	30	44	34	43	42	43	42	42	61	55	53	54	58	49	57	51	41	42	40	37	41	42

DG/ODW	85	67	70	52	59	41	48	55	34	39	14	37	37	23	29	not app	not app	not app	not app	not app	not app	not app
VG/ODW	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app
JW/ODW	46	31	35	34	33	30	32	33	32	32	31	33	31	33	32	27	30	32	35	32	35	38
MCL/JW	2	3	8	10	7	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app
A_1/ODW	90	82	88	53	49	52	50	59	30	39	21	35	36	22	28	53	52	51	49	50	45	50
$A_{1\ num}$	236	301	220	195	285	171	241	263	163	166	95	314	330	163	280	191	126	155	146	156	225	132
$A_{2\ num}$	237	270	208	253	290	236	325	316	394	302	265	681	526	485	642	212	156	193	210	238	307	177
$A_{3\ num}$ (R/L)	95/98	116/116	87/90	241	280	235	332	315	686	360	354	825	714	594	753	213	159	192	122	236	298	180
$A_{4\ num}$ (R/L)	68/70	94/89	77/76	230	270	204	291	278	391	329	385	786	556	489	754	189	152	171	130	204	262	163
$A_{5\ num}$ (R/L)	53/53	76/77	58/64	96/92	106/120	80/82	134/132	102/102	486	128/132	338	549	646	467	468	83/77	58/64	68/70	80/78	109/106	111/123	62/68
$A_{6\ num}$ (R/L)	28/28	56/54	37/40	62/64	89/90	60/58	92/91	72/71	157/162	82/84	138/150	232/276	261/254	186/162	270/296	44/49	44/44	32/34	62/59	88/95	89/83	43/46
$A_{7\ num}$	not app	30/16	not app	38/40	60/63	39/36	60/64	43/43	103/112	38/42	77/86	192/152	172/169	101/130	191/185	29/32	29/31	19/18	42/41	53/54	65/61	27/28
$A_{8\ num}$	not app	not app	not app	26/23	43/46	not app	not app	not app	51/52	38/43	32/30	85/68	96/98	62/61	93/92	not app	not app	not app	not app	not app	not app	not app
$P_{1\ num}$ (R/L)	80/82	187	84/82	169	203	124	176	161	328	282	208	339	330	315	450	153	121	126	150	187	184	116
$P_{2\ num}$	214	248	191	218	307	184	257	218	606	405	374	481	579	646	663	210	182	176	230	232	254	168
$P_{3\ num}$	256	356	232	376	562	293	245	337	740	590	311	1193	1052	1016	1204	432	223	325	367	423	393	239
MP	128	175	101	155	148	174	177	152	248	273	249	377	336	276	323	290	222	234	297	258	243	289
SMP	17/16	94	46/48	212	190	368	245	291	255	229	291	232	272	238	245	606	315	430	309	522	452	326
Total papillae	161	269	195	367	338	542	422	443	503	502	442	609	608	514	577	896	537	664	606	780	695	615
$A_{1\ den}$	74	80	67	75	115	102	104	102	112	102	128	122	125	129	150	92	76	84	83	81	126	107
$A_{2\ den}$	80	70	97	79	81	99	76	79	98	91	96	138	87	105	106	63	64	68	64	78	87	88
$A_{3\ den}$	77	143	60	66	78	81	72	77	170	108	118	167	117	129	125	64	48	56	35	55	67	72
$A_{4\ den}$	76	63	65	60	72	58	63	68	84	82	128	101	82	88	129	56	50	50	37	55	59	65
$A_{5\ den}$	84	71	71	54	62	60	60	57	98	64	104	67	89	85	66	65	52	59	61	69	61	63
$A_{6\ den}$	68	78	66	48	63	60	56	54	72	45	62	68	75	71	83	56	51	40	62	80	63	64
$A_{7\ den}$	not app	61	not app	52	59	52	53	52	64	34	78	66	61	61	73	70	56	35	74	69	73	67
$A_{8\ den}$	not app	not app	not app	58	55	not app	not app	not app	58	66	70	52	59	56	77	not app	not app	not app	not app	not app	not app	not app
$P_{1\ den}$	65	55	59	44	48	46	47	51	77	74	72	53	51	63	67	57	55	53	53	53	57	62
$P_{2\ den}$	80	65	68	53	67	68	61	61	128	100	122	70	83	118	90	69	72	60	60	55	72	81
$P_{3\ den}$	97	85	79	85	115	109	52	88	175	143	100	161	148	181	159	131	80	94	94	92	102	116
Jaw sheaths	A	A	A	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B	B
Upper sheath	C	C	C	C	C	C	C	C	D	D	D	D	D	D	D	C	C	C	C	C	C	C
Upper labium	G	G	G	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H	H

Table 4. Morphometric measurements (all in mm) of all *B. picturatus* and *B. majori* DNA voucher specimens described and used in this paper. For abbreviations, see Materials and Methods.

Species	*B. picturatus*	*B. picturatus*	*B. picturatus*	*B. picturatus*	*B. picturatus*	*B. majori*
Field number	FG/MV 2002/1835	ZCMV 5050	ZCMV 3487	ZCMV 3807	ZCMV 4941	ZCMV 2641
ZSM	821/2004	196/2007	1791/2007	172/2008	77/2008	397/2008
Date of capture	20.01.2003	06.03.2007	08.02.2006	28.02.2006	03.03.2007	20.02.2006
Site	Ranomafana	Ranomafana	An'Ala	Ranomena	Ambohitsara	Vohiparara
Stage	26	25	26	27	25	28
BL	11.7	13.6	11.3	13.7	9.7	9.4
BW	6.8	8.5	7.6	7.4	5.7	5.2
SBW	6.4	9.8	8.0	9.3	5.7	3.6
BH	5.0	6.2	5.5	6.3	4.1	3.8
SBH	7.8	8.8	8.5	9.3	6.2	6.9
ED	1.6	1.6	1.3	1.6	1.1	1.2
SE	3.4	5.0	3.6	4.3	2.6	2.7
EH	3.7	5.0	3.7	4.9	3.3	2.8
PP	3.6	4.5	3.8	4.3	2.8	3.6
ND	0.6	0.7	0.5	0.7	0.4	0.3
NH	3.2	4.7	3.4	4.9	3.3	2.6
NN	2.3	2.8	2.3	2.6	2.0	1.6
RN	1.6	2.7	1.8	2.2	1.4	1.1
NP	1.8	2.3	1.9	2.1	1.2	1.6
SL	2.6	1.3	2.0	1.7	0.7	1.2
SS	7.8	8.6	6.7	7.8	4.9	5.2
SV	3.9	5.1	4.8	4.5	4.8	4.2
SH	1.8	2.5	2.2	2.7	1.9	1.6
VL	2.4	2.5	2.6	2.5	1.7	0.6
TAL	21.2	23.5	16.5	22.9	14.9	10.0
TMW	3.1	4.1	3.1	4.2	2.1	2.0
TMH	3.3	4.3	3.1	4.5	2.2	2.6
TH	4.4	5.7	4.7	5.8	3.7	3.7
TMHM	2.0	2.6	1.9	3.2	1.3	2.0
THM	4.5	6.4	4.1	6.2	3.1	3.5
MTH	5.0	6.8	4.3	6.3	3.6	3.8
DMTH	7.8	9.3	6.6	10.5	5.6	2.9

UF	1.6	2.3	1.2	1.8	0.8	0.8
LF	1.0	1.5	1.0	1.2	1.0	0.7
HAB	3.2	4.4	3.2	4.6	2.9	2.1
TL	32.9	37.2	27.8	36.6	24.6	19.4

Table 5. Relative values (all in percentage) of all the morphometric parameters of all *B. picturatus* and *B. majori* DNA voucher specimens described and used in this paper. For abbreviations, see Materials and Methods.

Species	*B. picturatus*	*B. picturatus*	*B. picturatus*	*B. picturatus*	*B. picturatus*	*B. majori*
Field number	FG/MV 2002/1835	ZCMV 5050	ZCMV 3487	ZCMV 3807	ZCMV 4941	ZCMV 2641
ZSM	821/2004	196/2007	1791/2007	172/2008	77/2008	397/2008
Date of capture	20.01.2003	06.03.2007	08.02.2006	28.02.2006	03.03.2007	20.02.2006
Site	Ranomafana	Ranomafana	An'Ala	Ranomena	Ambohitsara	Vohiparara
Stage	26	25	26	27	25	28
BW/BL	59	62	67	54	59	55
SBW/BL	55	72	71	68	59	39
BW/BH	138	138	139	118	138	136
SBH/BL	67	64	75	68	64	74
ED/BL	14	12	12	12	11	13
SE/BL	29	36	32	31	27	29
EH/BH	74	81	67	78	81	75
PP/BW	53	52	51	58	50	69
ND/BL	5.0	5.1	4.2	5.1	4.6	2.7
NH/BH	65	76	62	79	80	68
RN/NP	90	120	97	105	116	69
NH/EH	87	93	93	101	99	91
NN/PP	63	63	60	59	69	44
SL/BL	22	10	18	12	7	12
SS/BL	67	63	59	57	51	55
SH/BH	37	41	40	43	46	42
SH/HAB	57	57	68	59	66	77
VL/BL	21	18	23	18	18	6
TAL/BL	182	173	146	168	154	107
TMW/BW	46	48	41	56	36	39
TMH/BH	66	69	57	71	53	68
TMH/MTH	65	63	73	71	60	68
TH/BH	88	93	86	92	91	97
TMHM/THM	43	40	47	51	41	56
TMHM/MTH	39	37	45	50	36	52
THM/BH	91	103	74	98	76	92
THM/MTH	91	94	95	98	87	93
MTH/BH	101	111	78	100	88	99
DMTH/TAL	37	39	40	46	38	29

UF/TMHM	83	90	61	56	62	42
LF/TMHM	51	60	50	39	77	37
UF/LF	164	149	122	142	81	111
HAB/BH	65	72	59	73	70	55

Table 6. Comparison of the oral disk characteristic of all *B. picturatus* and *B. majori* voucher specimens described and used in this paper. JW. MC. DG. A_1. A_2. $A_{2\ gap}$. $A_{row+gap}$. Kerat length. MP length and SMP length are in mm. ODW/BW. DG/ODW. JW/ODW. MCL/JW. A_1/ODW and A_2 gap/A_2 are in percentage. A_1 is a density per millimetre. UR. LR. A_1 num. MP. SMP and Tot pap are numbers. For abbreviations, see Materials and Methods.

Species	*B. picturatus*	*B. picturatus*	*B. picturatus*	*B. picturatus*	*B. picturatus*	*B. majori*
Field number	FG/MV 2002/1835	ZCMV 5050	ZCMV 3487	ZCMV 3807	ZCMV 4941	ZCMV 2641
ZSM	821/2004	196/2007	1791/2007	172/2008	77/2008	397/2008
Date of capture	20.01.2003	06.03.2007	08.02.2006	28.02.2006	03.03.2007	20.02.2006
Site	Ranomafana	Ranomafana	An'Ala	Ranomena	Ambohitsara	Vohiparara
Stage	26	25	26	27	25	28
ODW	3.53	4.2	3.5	4.0	3.1	1.9
LTRF	not app	not app	not app	not app	not app	1:4+4/1+1:2
UR	Abs	abs	abs	abs	abs	5
LR	Abs	abs	abs	abs	abs	3
JL	Abs	abs	abs	abs	abs	0.85
MC	Abs	abs	abs	abs	abs	0.41
DG	Abs	abs	abs	abs	abs	1.12
VG	Abs	abs	abs	abs	abs	abs
A_1 (R/L)	Abs	abs	abs	abs	abs	0.86
A_2	Abs	abs	abs	abs	abs	0.52/0.50
A_{2Gap}	Abs	abs	abs	abs	abs	0.11
$A_{2\ row+gap}$	Abs	abs	abs	abs	abs	1.13
A_3 (R/L)	Abs	abs	abs	abs	abs	0.28/0.26
A_4 (R/L)	Abs	abs	abs	abs	abs	0.24/0.24
A_5 (R/L)	Abs	abs	abs	abs	abs	0.20/0.21
P_1 (R/L)	Abs	abs	abs	abs	abs	0.62/0.69
P_2	Abs	abs	abs	abs	abs	1.05
P_3	Abs	abs	abs	abs	abs	0.91
Kerat length	Abs	abs	abs	abs	abs	0.06
MP lenght	0.08	0.08	0.15	0.1	0.07	0.10
SMP length	not app	not app	not app	not app	not app	not app
ODW/BW	52	50	47	54	55	58
DG/ODW	not app	not app	not app	not app	not app	58
VG/ODW	not app	not app	not app	not app	not app	not app
JW/ODW	not app	not app	not app	not app	not app	44
MCL/JW	not app	not app	not app	not app	not app	48
A_1/ODW	not app	not app	not app	not app	not app	45
A_2Gap/A_2Row	not app	not app	not app	not app	not app	10

A_1	Abs	abs	abs	abs	abs	50
A_2 (R/L)	Abs	abs	abs	abs	abs	26/27
A_3 (R/L)	Abs	abs	abs	abs	abs	20/19
A_4 (R/L)	Abs	abs	abs	abs	abs	18/18
A_5 (R/L)	Abs	abs	abs	abs	abs	14/16
P_1 (R/L)	Abs	abs	abs	abs	abs	46/45
P_2	Abs	abs	abs	abs	abs	76
P_3	Abs	abs	abs	abs	abs	76
MP	163	113	97	144	118	50
SMP	Abs	abs	abs	abs	abs	abs
Total papillae	163	113	97	144	118	50
A_1 den	not app	not app	not app	not app	not app	58
A_2 den	not app	not app	not app	not app	not app	98
A_3 den	not app	not app	not app	not app	not app	81
A_4 den	not app	not app	not app	not app	not app	75
A_5 den	not app	not app	not app	not app	not app	73
P_1 den	not app	not app	not app	not app	not app	69
P_2 den	not app	not app	not app	not app	not app	72
P_3 den	not app	not app	not app	not app	not app	70
OD orientation	A	A	A	A	A	A
Sheaths	C	C	C	C	C	D
MC	not app	not app	not app	not app	F	F

A: ventrally, **B:** anteroventrally;

C: absent, **D:** reduced;

F: very long narrowly pointed.

Table 7. Morphometric measurements (all in mm) of all DNA voucher specimens of tadpoles of *Mantidactylus* species in the subgenera *Ochthomantis* and *Maitsomantis* described in this paper. For abbreviations, see Materials and Methods.

Species	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. ambreensis*	*M. zolitschka*	*M. argenteus*	*M.* sp. 42	*M.* sp. 43	*M.* sp. 47	*M.* sp. 47	*M. mocquardi*	*M. mocquardi*	*M. mocquardi*	*M.* sp. 64	*M. majori*	*M. majori*
Field number	ZCMV 3431	T 2007-558	FGZC 2955	ZCMV 2640	TAD 2004-07	FG/MV 2002-1950	ZCMV 3565	ZCMV 3575	FG/MV 2002-1957	FGZC 2928	ZCMV 2699	TAD 2004-638	ZCMV 3511	ZCMV 4936	ZCMV 8094	ZCMV 2646	TAD 6 Vevembe	ZCMV 3761
ZSM	1736/2007	1928/2007	1630/2007	396/2008	1385/2004	762/2004	1843/2007	1573/2007	774/2004	1610/2007	456/2008	1198/2004	1540/2007	72/2008	686/2008	401/2008	1684/2007	1384/2004
Date of capture	08.02.2006	04.04.2007	19.02.2005	20.02.2006	10.02.2004	17.02.2003	08.02.2006	08.02.2006	17.02.2003	19.02.2003	26.01.2004	26.01.2004	08.02.2006	03.03.2007	13.02.2006	21.02.2006	10.02.2004	25.02.2006
Site	An'Ala	Isalo	Marojejy	Ranomafana	Vevembe	Ambre	An'Ala	An'Ala	Ambre	Marojejy	Imaloka	Maharira	An'Ala	Ambohitsara	Mahasoa	Namorona	Vevembe	*Sahamalaotra*
Gos	28	26	25	28	37	25	27	27	28	25	31	25	26	25	27	39	29	27
BL	11.4	12.2	6.4	10.2	12.7	5.7	9.2	12.2	11.1	7.0	12.1	8.2	11.4	7.0	13.8	10.8	13.1	13.5
BW	6.5	7.6	3.4	5.8	7.7	3.1	5.1	5.7	6.2	4.2	6.2	4.5	6.9	4.0	8.6	6.4	8.4	9.1
SBW	5.4	7.1	3.2	5.0	9.3	2.5	3.7	6.1	7.9	3.8	8.4	3.4	5.4	3.8	6.6	5.2	6.5	6.5
BH	4.6	5.0	2.6	3.5	5.4	2.5	3.4	5.2	5.1	3.0	4.8	3.2	4.6	2.8	6.4	4.7	5.7	6.5
SBH	8.0	7.3	4.4	7.9	9.3	3.4	6.5	6.8	7.6	5.0	8.3	5.5	8.3	4.6	11.2	7.5	8.9	10.3
ED	1.1	1.2	0.7	1.1	1.5	0.6	1.0	1.1	1.2	0.9	1.5	1.0	1.3	0.8	1.8	1.4	2.0	1.9
SE	3.7	3.5	2.2	3.2	3.2	2.1	2.8	2.6	3.1	2.8	3.1	2.5	4.0	2.6	4.4	2.9	4.9	5.3
EH	3.4	3.7	1.9	2.2	3.3	1.7	2.3	3.0	3.4	2.3	3.5	2.2	3.4	2.1	4.3	3.7	4.5	4.8
IOD	3.4	3.6	2.2	3.6	3.8	2.1	2.9	3.6	3.5	2.5	3.7	3.1	3.7	2.6	4.7	4.1	5.5	5.3
ND	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.1	0.2	0.1	0.2	0.1	0.3	0.4
NH	2.8	3.2	1.8	1.7	2.5	1.4	2.0	2.5	2.4	1.9	2.5	1.5	2.7	1.6	3.4	2.9	3.6	3.9
IND	2.0	2.0	1.2	2.1	2.3	1.4	1.8	1.9	2.0	1.4	2.2	1.9	2.5	1.7	3.3	2.0	3.0	3.1
RN	1.7	1.3	1.0	1.2	1.2	0.9	1.1	1.0	1.1	1.2	1.0	0.8	1.6	0.9	1.7	0.9	1.8	2.0
NP	2.0	2.2	1.2	2.1	2.1	1.3	1.7	1.5	2.0	1.6	2.1	1.8	2.4	1.6	2.8	2.1	3.1	3.3
SL	1.8	2.1	1.1	3.1	2.3	0.8	1.6	1.1	1.7	1.1	1.7	1.2	1.8	0.7	1.4	2.0	2.1	2.4
SS	7.4	7.5	4.2	7.9	7.8	4.1	5.7	6.6	6.9	5.2	6.7	5.2	7.7	5.1	9.8	7.0	9.9	11.2
SV	4.0	3.6	2.2	2.3	4.9	1.7	3.5	5.5	4.0	1.8	5.4	3.0	3.7	1.9	4.0	3.8	3.2	2.4
SH	3.2	3.0	1.4	1.4	2.8	1.4	1.4	2.5	2.8	1.5	2.4	1.6	1.9	1.3	3.0	2.5	2.2	2.9
VL	1.5	1.1	0.5	1.1	1.7	0.5	1.0	1.8	1.4	0.5	1.4	0.4	1.0	0.6	1.7	1.1	1.5	1.0
TAL	22.6	19.7	12.8	17.9	25.5	12.8	15.4	21.8	23.7	14.0	20.1	14.5	21.1	13.2	28.8	21.1	23.8	23.7
TMW	3.4	2.7	1.9	2.5	3.6	1.7	2.3	3.4	3.9	2.1	3.9	2.1	3.5	1.9	4.9	3.2	2.2	4.2
TMH	3.2	3.1	1.8	2.9	3.4	1.8	2.2	3.5	3.6	1.9	3.5	2.2	3.4	1.6	4.9	3.0	4.0	4.2
TH	4.0	4.1	2.4	3.3	4.8	2.1	3.2	4.3	4.9	2.8	4.3	2.6	4.2	2.5	6.2	4.2	5.1	5.8
TMHM	2.6	2.1	1.5	2.4	2.6	1.3	1.2	2.8	3.1	1.6	3.0	1.7	2.8	1.3	3.7	2.6	3.0	3.9
THM	4.4	3.9	2.8	4.2	5.4	2.1	3.4	5.0	5.3	3.2	4.4	2.6	4.7	2.8	6.9	4.8	5.4	7.5

MTH	5.1	4.3	2.9	4.3	5.5	2.3	3.6	5.5	5.4	3.3	4.8	3.0	4.7	2.9	6.9	4.9	5.8	7.6
DMTH	9.0	6.0	5.1	10.1	11.3	5.8	6.6	8.0	9.5	4.4	8.1	3.9	8.7	4.8	14.3	8.9	9.8	11.3
DF	1.0	1.0	0.7	1.1	1.4	0.4	1.0	1.2	1.2	0.9	0.8	0.5	1.2	1.0	1.9	1.2	1.6	2.4
VF	1.0	0.9	0.6	0.7	1.1	0.3	0.8	1.1	1.4	0.6	0.7	0.4	0.7	0.5	1.3	1.1	0.8	1.2
HAB	3.4	3.8	1.5	2.2	3.6	1.6	2.4	3.3	3.1	1.8	3.2	2.0	2.8	1.7	4.0	3.3	3.5	4.3
TL	34.0	31.9	19.2	28.1	38.2	18.4	24.6	34.0	34.8	21.0	32.1	22.7	32.5	20.2	42.6	31.9	36.9	37.3

Table 8. Relative values (%) of the morphometric parameters of the DNA voucher specimens of tadpoles of *Mantidactylus* species in the subgenera *Ochthomantis* and *Maitsomantis* described in this paper. For abbreviations, see Materials and Methods.

Species	***M. femoralis***	***M. femoralis***	***M. femoralis***	***M. femoralis***	***M. femoralis***	***M. ambreensis***	***M. zolitschka***	***M. argenteus***	***M.* sp. 42**	***M.* sp. 43**	***M.* sp. 47**	***M.* sp. 47**	***M. mocquardi***	***M. mocquardi***	***M. mocquardi***	***M.* sp. 64**	***M. majori***	***M. majori***
Field number	ZCMV 3431	T 2007-558	FGZC 2955	ZCMV 2640	TAD 2004-07	FG/MV 2002-1950	ZCMV 3565	ZCMV 3575	FG/MV 2002-1957	FGZC 2928	ZCMV 2699	TAD 2004-638	ZCMV 3511	ZCMV 4936	ZCMV 8094	ZCMV 2646	TAD 6 Vevembe	ZCMV 3761
ZSM	1736/2007	1928/2007	1630	396/2008	1385/2004	762/2004	1843/2007	1573/2007	774/2004	1610/2007	456/2008	1198/2004	1540/2007	72/2008	686/2008	401/2008	1684/2007	1384/2004
Date of capture	08.02.2006	04.04.2007	19.02.2005	20.02.2006	10.02.2004	17.02.2003	08.02.2006	08.02.2006	17.02.2003	19.02.2003	26.01.2004	26.01.2004	08.02.2006	03.03.2007	13.02.2006	21.02.2006	10.02.2004	25.02.2006
Site	An'Ala	Isalo	Marojejy	Ranomafana	Vevembe	Ambre	An'Ala	An'Ala	Ambre	Marojejy	Ambatolahy	Maharira	An'Ala	Ambohitsara	Mahasoa	Namorona	Ranomafana	Vevembe
Gos	28	26	25	28	37	25	27	27	28	25	31	25	26	25	27	39	29	27
BW/BL	57	62	53	57	61	55	55	47	56	60	52	55	60	58	63	59	64	67
SBW/BL	47	58	49	49	73	43	40	50	71	54	69	42	47	54	48	48	49	48
BW/BH	141	152	133	164	142	127	148	111	123	142	130	143	148	143	136	136	147	141
SBH/BL	70	60	69	77	73	60	71	56	68	71	69	67	73	66	81	69	68	77
ED/BL	10	10	11	11	12	11	11	9	11	13	13	12	12	11	13	13	15	14
SE/BL	32	28	34	32	25	37	30	21	28	39	26	31	35	36	32	27	38	39
EH/BH	73	73	73	61	62	68	68	58	67	78	73	69	73	73	67	79	78	75
IOD/BW	52	47	66	61	50	66	56	63	55	59	59	69	53	65	54	64	66	58
ND/BL	1.1	1.1	1.7	1.1	0.9	2.3	1.3	0.8	1.1	2.0	1.1	1.1	1.4	2.0	1.6	1.3	2.5	3.3
NH/BH	60	63	69	49	46	58	58	48	47	65	53	49	59	58	53	62	64	60
RN/NP	83	61	82	57	57	67	61	68	57	76	48	43	67	57	59	43	59	59
NH/EH	83	86	95	81	75	85	86	84	70	84	72	71	81	79	79	79	81	81
IND/IOD	58	56	55	59	60	65	64	54	57	58	58	60	68	64	70	48	53	58
SL/BL	16	17	17	30	18	14	17	9	15	15	14	14	16	11	10	19	16	18
SS/BL	65	62	66	77	61	72	62	55	62	75	56	63	67	73	71	64	76	83
SH/BH	69	60	56	40	52	55	40	49	55	52	51	50	42	45	48	54	38	45
SH/HAB	96	80	93	66	79	85	58	77	89	85	76	81	70	76	76	76	61	67
VL/BL	13	9	8	11	13	9	11	14	13	7	11	5	9	8	12	10	11	7
TAL/BL	198	161	200	175	200	225	167	180	214	201	166	176	185	189	209	196	181	176
TMW/BW	52	35	56	44	46	55	45	60	62	49	63	47	51	46	56	50	26	46
TMH/BH	68	63	71	82	62	74	64	67	72	64	73	71	74	56	78	64	70	66
TMH/MTH	62	73	62	67	61	79	61	63	67	58	73	75	73	54	71	62	69	56
TH/BH	85	82	95	95	90	85	92	84	96	94	90	83	91	87	97	89	89	90
TMHM/THM	58	53	53	56	48	62	34	55	58	51	67	65	60	46	54	55	56	53

TMHM/MTH	50	48	50	55	47	55	33	51	57	50	62	56	59	44	54	53	52	52
THM/BH	95	78	109	120	99	83	100	97	105	107	90	82	91	99	97	89	94	116
THM/MTH	87	91	95	98	97	88	96	92	98	96	93	87	99	96	100	97	93	98
MTH/BH	109	86	115	123	102	94	105	106	107	111	100	95	102	103	109	103	101	118
DMTH/TAL	40	31	40	57	44	45	43	37	40	31	40	27	42	36	50	42	41	47
DF/TMHM	40	47	48	46	56	33	82	43	40	57	28	32	41	75	52	44	53	60
VF/TMHM	37	42	41	31	43	27	68	41	45	39	24	24	25	42	34	42	27	29
DF/VF	107	111	115	151	131	124	122	104	87	148	117	133	162	178	154	106	195	205
HAB/BH	72	75	60	61	66	65	70	64	62	60	67	62	60	60	63	70	62	67

Table 9. Comparison of the oral disk characteristics of the voucher specimens of tadpoles of *Mantidactylus* species in the subgenera *Ochthomantis* and *Maitsomantis* described in this paper. JW, Thorn-pap, MCL, DG, $A_{1\text{-}2\ len}$, $P_{1\text{-}3\ len}$, $A_{2\ gap}$, $A_{2\ row+gap}$, Kerat len, MP len and SMP len are in mm. ODW/BW, DG/ODW, JW/ODW, MCL/JW, A_1/ODW and A_2Gap/A_2 are in %. $A_{1\text{-}2\ den}$, $P_{1\text{-}3\ den}$, is density (number/mm). UR, LR, A_1 num, MP, SMP and Tot pap are total numbers. A: ventrally; B: anteroventrally; C: soft partially keratinised with smooth surface; D: thorn-shaped papillae, not keratinized; E: lower sheath totally hidden; F: short widely pointed; G: short widely rounded; H: moderately long widely pointed; I: moderately long widely rounded; J: moderately long narrowly pointed; K: long narrowly pointed; L: very long narrowly pointed; M: upper labium is a continuation of the snout; N: anterior margin is separated by a shallow crevice; O: moderately long with rounded tip; P: long, MP rounded tip, SMP pointed tip; Q: long, with pointed tip (MP and SMP); R: scattered and forming chevron; S: lower row absent; not app: not applicable; abs: absent. For further abbreviations, see Material and methods.

Species	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. femoralis*	*M. ambreensis*	*M. zolitschka*	*M. argenteus*	M. sp. 42	M. sp. 43	M. sp. 47	M. sp. 47	*M. mocquardi*	*M. mocquardi*	*M. mocquardi*	M. sp. 64	*M. majori*	*M. majori*
Field number	ZCMV 3431	T 2007-558	FGZC 2955	ZCMV 2640	TAD 2004-07	FG/MV 2002-1950	ZCMV 3565	ZCMV 3575	FG/MV 2002-1957	FGZC 2928	ZCMV 2699	TAD 2004-638	ZCMV 3511	ZCMV 4936	ZCMV 8094	ZCMV 2646	TAD 6 Vevembe	ZCMV 3761
ZSM	1736/2007	1928/2007	1630	396/2008	1385/2004	762/2004	1843/2007	1573/2007	774/2004	1610/2007	456/2008	1198/2004	1540/2007	72/2008	686/2008	401/2008	1684/2007	1384/2004
Date of capture	08.02.2006	04.04.2007	19.02.2005	20.02.2006	10.02.2004	17.02.2003	08.02.2006	08.02.2006	17.02.2003	19.02.2003	26.01.2004	26.01.2004	08.02.2006	03.03.2007	13.02.2006	21.02.2006	10.02.2004	25.02.2006
Site	An'Ala	Isalo	Marojejy	Ranomafana	Vevembe	Ambre	An'Ala	An'Ala	Ambre	Marojejy	Ambatolahy	Maharira	An'Ala	Ambohitsara	Mahasoa	Namorona	Ranomafana	Vevembe
Gos	28	26	25	28	37	25	27	27	28	25	31	25	26	25	27	39	29	27
ODW	2.8	2.5	1.6	2.2	3.0	1.1	2.0	1.8	2.3	2.0	2.3	2.1	3.0	1.7	4.0	2.2	3.4	3.4
LTRF	3(2-3)/3(1-2)	3(2-3)/3(1-2)	3(2-3)/3(1-2)	3(2-3)/3(1-2)	3(2-3)/3(1-2)	2(2)/3(1-2)	3(2-3)/3(1-2)	2(2)/3(1-2)	3(2-3)/3(1-2)	2(2)/3(1-2)	3(2-3)/3(1-2)	3(2-3)/3(1-2)	not app	not app	not app	not app	not app	not app
UR	3	3	3	3	3	2	3	2	3	2	3	3	not app	not app	not app	not app	not app	not app
LR	3	3	3	3	3	3	3	3	3	3	3	3	not app	not app	not app	not app	not app	not app
JW	1.3	1.1	0.6	1.2	1.1	0.6	1.0	0.8	1.2	0.8	1.2	0.9	1.3	0.5	1.9	1.2	1.8	1.7
Thorn-pap	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	not app	0. 6/0.8/0.7	0.5/0.7/0.5
MCL	0.24	0.23	0.14	0.25	0.30	0.10	0.29	0.25	0.21	0.20	0.23	0.19	0.28	0.24	0.57	0.26	not app	not app
DG	1.32	1.41	0.86	1.37	1.24	0.73	1.12	1.09	1.06	1.03	1.00	0.92	abs	abs	abs	abs	abs	abs
VG	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs	abs
$A_{1\ len}$	1.23	1.49	1.02	1.34	0.97	0.72	0.93	1.15	0.74	0.98	0.95	0.76	abs	abs	abs	abs	abs	abs
$A_{2\ len}$ (R/L)	0.20/0.22	0.23/0.18	0.24/0.29	0.29/0.26	0.16/0.22	0.12/0.13	0.20/0.19	0.14/0.20	0.07/0.12	0.15/0.17	0.16/0.11	0.11/0.16	abs	abs	abs	abs	abs	abs
A_{2Gap}	0.83	1.06	0.44	0.85	0.98	0.49	0.72	0.58	0.86	0.73	0.84	0.60	abs	abs	abs	abs	abs	abs
$A_{2\ row+gap}$	1.25	1.47	0.97	1.40	1.36	0.84	1.11	0.92	1.05	1.10	1.11	0.87	abs	abs	abs	abs	abs	abs
$A_{3\ len}$ (R/L)	0.11/0.14	0.07/0.11	0.12/0.14	0.20/0.19	0.16/0.19	abs	0.14/0.08	abs	0.07/0.06	abs	0.50/0.50	0.13/0.15	abs	abs	abs	abs	abs	abs
$P_{1\ len}$ (R/L)	0.59/0.61	0.56/0.57	0.43/0.45	0.55/0.50	0.72/0.62	0.30/0.27	0.60/0.45	0.28/0.27	0.52/0.56	0.34/0.40	0.50/0.43	0.41/0.47	abs	abs	abs	abs	abs	abs
$P_{2\ len}$ (R/L)	0.57/0.65	0.62/0.48	0.47/0.44	0.62/0.50	0.57/0.50	0.26/0.26	0.66/0.34	0.4570.43	0.45/0.42	0.21/0.25	0.45/0.34	0.47/0.50	abs	abs	abs	abs	abs	abs
$P_{3\ len}$	0.57	1.12	0.57	0.41	0.38	0.31	0.25	0.19	0.87	0.09	0.25	0.49	abs	abs	abs	abs	abs	abs
Kerat len	0.06	0.06	0.06	0.07	0.08	0.04	0.05	0.06	0.09	0.07	0.05	0.04	not app	not app	not app	not app	not app	not app
MP len	0.17	0.10	0.09	0.09	0.12	0.08	0.10	0.15	0.13	0.10	0.14	0.09	0.19	0.09	0.25	0.11	0.25	0.22
SMP len	0.16	0.13	0.08	0.11	0.20	0.08	0.15	0.07	0.14	0.08	0.11	0.10	0.25	0.12	0.35	0.15	0.41	0.52
ODW/BW	42	32	46	38	39	35	40	31	36	46	36	47	43	42	47	34	40	38
DG/ODW	48	58	55	63	41	66	56	62	47	53	44	43	abs	abs	abs	abs	abs	abs

JW/ODW	49	46	37	53	35	53	47	43	52	41	51	39	43	32	48	56	54	51
MCL/JW	18	21	24	22	28	17	31	33	18	25	20	23	22	44	30	21	not app	not app
A_1/ODW	45	61	65	62	32	65	46	65	33	51	42	36	not app	not app	not app	not app	not app	not app
A_2Gap/A_2	66	72	45	61	72	58	65	63	82	66	76	69	not app	not app	not app	not app	not app	not app
$A_{1\ num}$	48	50	55	43	39	21	25	41	12	13	14	23	abs	abs	abs	abs	abs	abs
$A_{2\ num}$ (R/L)	10/10	10/7	12/13	10/10	8/11	6/6	7/8	5/6	4/6	8/10	5/5	5/6	abs	abs	abs	abs	abs	abs
$A_{3\ num}$ (R/L)	7/6	3/5	5/7	10/11	5/9	abs	7/3	abs	4/3	abs	2/2	12	abs	abs	abs	abs	abs	abs
$p_{1\ num}$ (R/L)	28/29	20/20	24/24	30726	42/38	12/13	22/25	8/9	24/21	14/16	19/17	17/18	abs	abs	abs	abs	abs	abs
$P_{2\ num}$ (R/L)	21/24	21/15	21/22	30/28	22/25	13/14	20/20	16/15	19/19	10/12	18/13	21/21	abs	abs	abs	abs	abs	abs
$P_{3\ num}$	20	15	27	17	15	10	11	5	13	5	9	24	abs	abs	abs	abs	abs	abs
MP	59	50	43	59	71	30	69	31	53	78	72	64	74	64	89	81	72	105
SMP	69	69	30	65	60	18	46	18	42	50	66	58	104	77	88	87	135	201
Total pap	128	119	73	124	131	48	115	49	95	128	138	122	178	141	177	168	207	306
$A_{1\ den}$	39	34	53	32	40	29	27	36	16	13	15	30	not app	not app	not app	not app	not app	not app
$A_{2\ den}$	48	33	47	54	53	abs	38	32	53	56	35	39	abs	abs	abs	abs	abs	abs
$A_{3\ den}$	50	44	46	44	38	abs	46	abs	54	abs	40	43	abs	abs	abs	abs	abs	abs
$p_{1\ den}$	48	35	55	53	60	44	45	31	38	41	39	40	abs	abs	abs	abs	abs	abs
$P_{2\ den}$	37	32	47	52	45	52	40	35	44	63	39	43	abs	abs	abs	abs	abs	abs
$P_{3\ den}$	35	39	47	41	39	32	44	26	30	56	36	49	abs	abs	abs	abs	abs	abs
OD orient	B	A	A	A	A	B	B	B	B	B	B	A	B	B	A	B	A	A
Up sheaths	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	C	D	D
Low sheath	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E	E
MC	G	I	G	I	I	F	K	K	G	H	H	H	J	L	L	G	not app	not app
Up labium	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	M	N	N
Papillae	O	O	O	O	O	O	O	O	O	O	O	O	P	P	P	P	Q	Q
Lower row	R	R	R	R	R	R	R	R	R	R	R	R	S	S	S	S	S	S

Table 10. Morphometric measurements (all in mm) of *Gephyromantis* DNA voucher specimens described in this paper. For abbreviations, see Materials and Methods.

Species	*G. granulatus*	*G. sculpturatus*	*G. tschenki*	*G ventrimaculatus*	*G. ambohitra*	*G. pseudoasper*
Field number	Tad 2004-0075	ZCMV4833	ZCMV4335	ZCMV4927	FG/MV 2002-1946	FG/MV 2002-1919
ZSM	298/2008	16/2008	142/2007	852/2007	756/2004	707/2004
Date of capture	19-23.02.2004	11.02.2007	25.02.2007	20.03.2007	17.02.2003	01.02.2003
Site	Mt d'Ambre	Ranomafana	Ranomafana	Ranomafana	Mt d'Ambre	Manongarivo
GOS	40	39	35	39	40	39
BL	5.8	6.0	4.6	6.4	9.7	14.0
BW	3.2	3.5	2.6	3.6	5.6	10.2
SBW	2.5	3.0	2.9	2.9	4.9	9.8
BH	2.4	2.5	2.3	3.1	4.5	7.4
SBH	3.6	3.8	2.8	4.2	6.8	9.6
ED	1.0	1.2	0.8	1.1	1.3	2.3
SE	1.5	1.4	0.9	1.5	2.5	5.1
EH	1.4	1.6	1.4	1.9	3.3	5.2
IOD	2.2	2.6	1.6	2.8	3.3	5.2
ND	0.08	0.10	0.09	0.11	0.29	0.33
NH	0.8	1.0	0.9	1.4	2.5	4.6
IND	1.2	1.2	1.1	1.3	1.6	3.2
RN	0.4	0.4	0.3	0.7	0.8	2.2
NP	1.0	1.1	0.6	0.8	1.7	2.9
SL	0.8	0.5	0.4	0.4	1.4	2.3
SS	3.4	3.8	2.3	3.5	5.5	10.3
SV	2.4	2.8	2.4	2.9	4.2	3.7
SH	0.9	0.9	0.9	1.0	1.9	3.0
VL	0.8	0.7	0.8	0.6	1.5	1.6
TAL	17.6	18.2	14.0	20.4	17.3	36.3
TMW	2.5	1.9	1.2	2.0	2.5	4.8
TMH	1.6	1.8	1.3	1.8	2.3	4.5
TH	1.6	2.0	1.7	1.9	3.9	5.7
TMHM	1.8	1.7	1.3	2.2	1.9	3.7
THM	2.6	2.6	2.0	3.0	4.0	7.3
MTH	2.7	2.6	2.2	3.0	4.5	7.4
DMTH	12.1	11.0	9.7	12.9	6.6	12.9
DF	0.3	0.3	0.3	0.4	1.1	2.0
VF	0.4	0.6	0.3	0.4	1.0	1.7
HAB	1.5	1.6	1.4	1.8	2.5	4.5

TL	20.7	21.6	16.7	24.0	22.9	46.4

Table 11. Morphometric ratios (in %) of *Gephyromantis* DNA voucher specimens described in this paper. For abbreviations see Materials and Methods.

Species	*G. granulatus*	*G. sculpturatus*	*G. tschenki*	*G ventrimaculatus*	*G. ambohitra*	*G. pseudoasper*
Field number	Tad 2004-0075	ZCMV4833	ZCMV4335	ZCMV4927	FG/MV 2002-1946	FG/MV 2002-1919
ZSM	298/2008	16/2008	142/2007	852/2007	756/2004	707/2004
Date of capture	19-23.02.2004	11.02.2007	25.02.2007	20.03.2007	17.02.2003	01.02.2003
Site	Mt d'Ambre	Ranomafana	Ranomafana	Ranomafana	Mt d'Ambre	Manongarivo
GOS	40	39	35	39	40	39
BW/BL	55	58	57	56	58	73
SBW/BL	44	50	64	45	51	70
BW/BH	132	138	117	117	123	137
SBH/BL	62	63	60	65	70	69
ED/BL	17	19	17	16	14	16
SE/BL	25	24	19	23	26	36
EH/BH	61	64	63	59	72	70
IOD/BW	68	74	62	76	59	51
ND/BL	1	2	2	2	3	2
NH/BH	33	41	40	45	55	62
RN/NP	42	34	55	86	50	76
NH/EH	55	63	65	75	77	89
IND/IOD	56	47	65	48	48	62
SL/BL	14	8	9	6	14	16
SS/BL	59	63	50	54	57	74
SH/BH	39	36	39	32	42	40
SH/HAB	61	56	64	54	75	66
VL/BL	14	11	18	10	15	12
TAL/BL	305	303	303	316	179	260
TMW/BW	80	53	47	54	45	47
TMH/BH	66	70	60	59	50	61
TMH/TH	100	88	81	94	60	61
TMH/MTH	58	66	60	60	51	61
TH/BH	66	80	73	62	86	77
TMHM/THM	72	66	68	72	48	50
TMHM/MTH	67	66	60	71	42	50
THM/BH	108	105	87	96	87	99
THM/MTH	94	100	88	98	89	99
MTH/BH	115	106	100	97	98	100
DMTH/TAL	69	61	69	64	38	35

DF/VF	81	61	114	86	110	117
DF/TMHM	18	20	25	18	57	54
VF/TMHM	23	32	22	20	52	46
HAB/BH	64	65	60	58	56	61

Table 12. Comparison of the oral disk characteristic of *Gephyromantis* voucher specimens described in this paper. JW, MCL, DG, $A_{1\text{-}5\ len}$, $P_{1\text{-}3\ len}$, $A_{2\ gap}$, $A_{row+gap}$, Kerat length, MP lenght and SMP length are in mm. ODW/BW. UR, LR, $A_{1\text{-}5\ num}$, $P_{1\text{-}3\ num}$ MP, SMP and Tot pap are numbers. DG/ODW, JW/ODW, MCL/JW, A_1/ODW and A_2Gap/A_2 are in %. $A_{1\text{-}5\ den}$ and $P_{1\text{-}3\ den}$ are density (number/mm). **A:** ventrally, **B:** anteroventrally; **C:** absent, **D:** generalized, **E**: hypertrophied; **F:** very short and widely rounded, **G:** very short and widely pointed; **H:** upper labium has no connection with snout, **I:** upper labium is a continuation of the snout; **J:** small with rounded tip, **K:** moderately large with rounded tip, **L:** large with pointed tip; **not app:** not applicable, **abs:** absent. For abbreviations, see Materials and Methods.

Species	*G. granulatus*	*G. sculpturatus*	*G. tschenki*	*G ventrimaculatus*	*G. ambohitra*	*G. pseudoasper*
Field number	Tad 2004-0075	ZCMV4833	ZCMV4335	ZCMV4927	FG/MV 2002-1946	FG/MV 2002-1919
ZSM	298/2008	16/2008	142/2007	852/2007	756/2004	707/2004
Date of capture	19-23.02.2004	11.02.2007	25.02.2007	20.03.2007	17.02.2003	01.02.2003
Site	Mt d'Ambre	Ranomafana	Ranomafana	Ranomafana	Mt d'Ambre	Manongarivo
GOS	40	39	35	39	40	39
ODW	0.5	0.3	0.3	0.7	2.1	3.5
LTRF	not app	not app	not app	not app	5(2-5)/3(1)	1/2(1)
UR	not app	not app	not app	not app	5	1
LR	not app	not app	not app	not app	3	2
JW	not app	not app	not app	not app	1.12	1.60
MCL	not app	not app	not app	not app	0.02	0.06
DG	not app	not app	not app	not app	1.58	1.03
VG	not app	not app	not app	not app	abs	abs
$A_{1\ len}$	abs	abs	abs	abs	1.78	0.96
$A_{2\ len}$	abs	abs	abs	abs	0.87/0.84	abs
A_{2Gap}	abs	abs	abs	abs	0.10	abs
$A_{2\ row+gap}$	abs	abs	abs	abs	1.81	abs
$A_{3\ len}$	abs	abs	abs	abs	0.69/0.65	abs
$A_{4\ len}$	abs	abs	abs	abs	0.51/0.47	abs
$A_{5\ len}$	abs	abs	abs	abs	0.25/0.18	abs
$P_{1\ len}$	abs	abs	abs	abs	0.78/0.80	0.54/0.52
$P_{2\ len}$	abs	abs	abs	abs	2.77	0.77
$P_{3\ len}$	abs	abs	abs	abs	1.76	abs
Kerat length	not app	not app	not app	not app	0.12	0.08
MP lenght	not app	not app	not app	not app	0.12	0.57
SMP length	not app	not app	not app	not app	0.11	0.27
ODW/BW	15	8	10	19	38	34
DG/ODW	not app	not app	not app	not app	75	30
VG/ODW	not app	not app	not app	not app	abs	abs
JW/ODW	not app	not app	not app	not app	53	46
MCL/JW	not app	not app	not app	not app	2	4
A_1/ODW	not app	not app	not app	not app	85	28

A_2Gap/A_2Row	not app	not app	not app	not app	6	abs
$A_{1\ num}$	abs	abs	abs	abs	150	40
$A_{2\ num}$	abs	abs	abs	abs	62/62	abs
$A_{3\ num}$	abs	abs	abs	abs	45/43	abs
$A_{4\ num}$	abs	abs	abs	abs	36/33	abs
$A_{5\ num}$	abs	abs	abs	abs	17/11	abs
$P_{1\ num}$	abs	abs	abs	abs	53/52	24/21
$P_{2\ num}$	abs	abs	abs	abs	132	40
$P_{3\ num}$	abs	abs	abs	abs	143	abs
MP	abs	-	abs	abs	63	39
SMP	abs	-	abs	abs	5/5	72
Total papillae	abs	4	abs	abs	73	111
$A_{1\ den}$	not app	not app	not app	not app	84	42
$A_{2\ den}$	not app	not app	not app	not app	93	abs
$A_{3\ den}$	not app	not app	not app	not app	90	abs
$A_{4\ den}$	not app	not app	not app	not app	70	abs
$A_{5\ den}$	not app	not app	not app	not app	65	abs
$P_{1\ den}$	not app	not app	not app	not app	66	42
$P_{2\ den}$	not app	not app	not app	not app	48	52
$P_{3\ den}$	not app	not app	not app	not app	81	abs
OD orientation	A	A	A	A	A	B
Sheaths	C	C	C	C	D	E
MC	not app	not app	not app	not app	F	G
Upper labium	H	H	H	H	I	I
Papillae	abs	abs	abs	abs		
Lower row	abs	J	abs	abs	K	L

Table 13. Classification of character states.

No	Characters	0	1	2	3	4	5
1	Body shape: body width (BW) vs body heigth (BH)	< 100% (compressed)	> 100% (depressed)				
2	Body form in dorsal view	ovoid	elliptical	rounded			
3	BW vs BL	< 50%	50-60%	60-70%	>70%		
4	Maximal body width location SBW vs BL	in the proximal 1/5 of the body (<20%)	in the proximal 1/5 to 2/5 of the body (20 - 40%)	in the proximal 2/5 to 3/5 of the body (40 - 60%)	in the proximal 3/5 to 4/5 of the body (60 - 80%)	in the distal 1/5 of the body (>80%)	
5	Maximal body heigth location SBH vs BL	in the proximal 1/5 of the body (<20%)	in the proximal 1/5 to 2/5 of the body (20 - 40%)	in the proximal 2/5 to 3/5 of the body (40 - 60%)	in the proximal 3/5 to 4/5 of the body (60 - 80%)	in the distal 1/5 of the body (>80%)	
6	Snout (dorsal view)	pointed = sharped	narowly rounded	broadly rounded	flatly rounded	rounded snout with protuberation	
7	Snout (lateral view)	pointed = sharped	narowly rounded	broadly rounded	flatly rounded		
8	Eyes size (ED) vs body lenght (BL)	< 10% (small)	10 - 15% (moderately large)	15 - 20% (large)	> 20% (very large)		
9	Eyes position	laterally	dorsally				
10	Eyes situation SE vs BL	in the 1/10 proximal of the body (< 10%)	between the proximal 1/10 and 2/10 of the body (10 - 20%)	(20 - 30%)	(30 - 40%)	(40 - 46%)	at mid-body (> 47%)
11	Eyes height (EH vs BH)	< 20% (very low)	20 - 40% (low)	40 - 60% (moderately high)	60 - 80% (high)	> 80% (very high)	
12	Eyes orientation	laterally	dorsolaterally	dorsally			
13	IOD vs BW	< 20% (very narrow)	20 - 40% (narrow)	40 - 60% (moderately wide)	60 - 80% (wide)	> 80% (very wide)	
14	Eyes visibily from ventral view	no	yes				
15	Nares size (ND) vs body length (BL)	< 1% (very small)	1 - 2% (small)	2 - 3% (moderately large)	3 - 4 % (large)	> 4% (very large)	
16	Nares postition	dorsally	laterally	ventrally			
17	Nares location (RN vs NP)	nearer snout than eyes < 100%	equidistant beteen snout and eyes = 100%	nearer eyes than snout > 100%			
18	Nares height (NH vs BH)	< 20% (very low)	20 - 40% (low)	40 - 60% (moderately high)	60 - 80% (high)	> 80% (very high)	
19	Nares position vs eye position (NH vs EH)	< 96% below the eye level	97-103% at the eye level	> 104% above the eye level			
20	Narial opening direction1 (horizontal plan)	anteriorly	anterolaterally	laterally	ventrolaterally	ventrally	
21	Narial opening direction2 (vertical plan)	dorsally	dorsolaterally	laterally	ventrolaterally	ventrally	
22	Narial opening configuration	flush with the surronding surface	countersunk	marked with a marginal rim			
23	Narial opening form	rounded	oval	elliptical	roughly triangular		
24	Narial ornamentations	narine non saillantes	narines saillantes sans ornementation	extension peau formant toit sur partie >	small mediodorsal projection		
25	Dark spot on the back of the nares	absent	present				
26	Nostril distance (IND) vs Interorbital distance (IOD)	< 20% (very narrow)	20 - 40% (narrow)	40 - 60% (moderately wide)	60 - 80% (wide)	> 80% (very wide)	
27	Spiracle type	sinistral	ventrally				
28	Spiracle length (SL) vs body length (BL)	< 10% (very short)	10 - 20% (short)	20 - 30% (modeartely long)	30 - 40% (long)	> 40% very long	
29	Spiracle location (SS vs BL)	in the proximal 1/5 of the body (<20%)	in the proximal 1/5 to 2/5 of the body (20 - 40%)	in the proximal 2/5 to 3/5 of the body (40 - 60%)	in the proximal 3/5 to 4/5 of the body (60 - 80%)	in the distal 1/5 of the body (>80%)	
30	Spiracle height (SH vs BH)	< 20% (very low)	20 - 40% (low)	40 - 60% (moderately high)	60 - 80% (high)	> 80% (very high)	

31	Spiracle opening height (SH) vs (HAB)	< 50% (at the height of the hindlimb insertion)	50 - 100%	100%	> 100%		
32	Spiracle opening direction	dorsally	posterodorsally	posteriorly			
33	Spiracle opening configuration	inner wall absent	inner wall persent as a slight ridge	inner wall free from body aperture opens posteriorly	inner wall free, aperture opens laterally		
34	Spiracle opening shape	rounded	elliptical				
35	Spiracle visibility from dorsal and ventral view	visible only from dorsal view	visible only from ventral view	visible from dorsal and ventral views	not visible from dorsal neither ventral view		
36	Spiracle visibility from lateral view	not visible	perceivable	obvious, distinguish, distinct, clear, evident			
37	Vent tube length (VL) vs body length (BL)	< 5% (very short)	5 - 10% (short)	10 - 15% (moderately long)	15 - 20% (long)	> 20% (very long)	
38	Vent tube in association with ventral fin	no	yes				
39	Medial vent tube opening configuration	dextral	medial without web between	medial with web between	medial with lateral displacement	medial without association with ventral fin	medial opens direclty at the end of the body
40	Dextral vent tube opening configuration	medial	dextral, inner wall present	dextral inner wall absent			
41	Intestine visibility	not visible	transparent	translucent			
42	Intestine spirale shaped	not visible	regular	irregular			
43	Gland	absent	present				
44	Tail length (TAL) vs body length (BL)	< 150% (very short)	150 - 200% (short)	200 - 250% (moderately long)	250 - 300% (long)	> 300% (very long)	
45	Tail muscle width at the body-tail junction (TMW) vs body width (BW)	< 20% (very narrow)	20 - 40% (less developed)	40 - 60% (moderately developped)	60 - 80% (developed)	> 80% (well developed)	
46	Tail muscle heigth at the body-tail junction (TMH) vs body heigth (BH)	< 20% (very low)	20 - 40% (less developed)	40 - 60% (moderately developped)	60 - 80% (developed)	> 80% (well developed)	
47	Tail muscle height at mid-tail (TMHM) vs tail heigth at mid tail (THM)	< 20% (very low)	20 - 40% (less developed)	40 - 60% (moderately developped)	60 - 80% (developed)	80 - 99% (well developed)	100% (no fin at mid-tail)
48	Tail heigth at midtal (TMHM) vs maximal tail heigth (MTH)	< 20% (very low)	20 - 40% (less developed)	40 - 60% (moderately developped)	60 - 80% (developed)	> 80% (well developed)	
49	Maximal tail heigth (MTH) vs body heigth (BH)	< 96% (lower)	97-103% (almost the same height = as high as)	> 104% (higher)			
50	Tail muscle height (TMH) vs maximal tail heighr (MTH)	< 20% (very low)	20 - 40% (less developed)	40 - 60% (moderately developped)	60 - 80% (developed)	> 80% (well developed)	
51	Tail height (TH) vs body height (BH)	< 96% (lower)	97-103% (almost the same height = as high as)	> 104% (higher)			
52	Tail height at midtail (THM) vs body height (BH)	< 96% (lower)	97-103% (almost the same height = as high as)	> 104% (higher)			
53	Tail height at midtail (THM) vs maximal tail heigth (MTH)	< 96% (lower)	97-100% (THM = MTH)				
54	Maximal tail heigth location (DMTH vs TAL)	in the proximal 1/5 of the tail (<20%)	in the proximal 1/5 to 2/5 of the tail (20 - 40%)	in the proximal 2/5 to 3/5 of the tail (40 - 60%)	in the proximal 3/5 to 4/5 of the tail (60 - 80%)	in the distal 1/5 of the tail (>80%)	
55	Tail muscle reaches tail extremity	no	yes				
56	Lateral tail vein visibility	not visible	untill the proximal 1/4 of the tail	untill the 1/2 of the tail	untill the 3/4 of the tail	reaching the tail tip	
57	(HAB vs BH)	< 20% (very low)	20 - 40% (low)	40 - 60% (moderately high)	60 - 80% (high)	> 80% (very high)	
58	Axis of the body length and axis of the tail myotomes	parallel	not parallel				
59	Dorsal fin type (DF vs TMHM)	< 50% (very low)	50 - 100% (low)	100 - 150% (moderately high)	150 - 200% (high)	> 200% (very high)	
60	Ventral fin type (VF vs TMHM)	< 50% (very low)	50 - 100% (low)	100 - 150% (moderately high)	150 - 200% (high)	> 200% (very high)	
61	Dorsal fin (DF) vs ventral fin (VF)	< 96% (lower)	97-103% (almost the same height = as high as)	> 104% (higher)			
62	Dorsal fin origins at	anterior to dorsal body-tail junction	dorsal body-tail junction	between the dorsal body-tail and the proximal 1/4 of tail	between the prox 1/4 and the 1/2 tail	in the distal 1/2 of tail	
63	Ventral fin orgins at	anterior to ventral body-tail junction	ventral body-tail junction	between the vetral body-tail and the proximal 1/4 of tail	between the prox 1/4 and the 1/2 tail	in the distal 1/2 of tail	

64	Tail tip	pointed	narowly rounded	broadly rounded			
65	Oral disk type	generalized	enlarged	reduced	umbelliform	highly modified	just a small opening
66	Emargination	emarginated	not emarginated	not applicable			
67	Labia width	in the middle	upper labium is wider than lower labium	lower labium is wider than upper labium	two labia have the same width		
68	Oral disk width (ODW) vs body width (BW)	< 20% (very small)	20 - 40% (small)	40 - 60% (moderately large)	60 - 80% (large)	80 - 100% (very large)	> 100% (hyperlarge)
69	Upper labium & Body wall	upper labium is a continuation of snout	anterior margin is separated by a shallow crevice	anterior margin separated by a deep crevice	umbrella	od has no connection with snout	
70	Oral disc position	ventrally	antéroventrally	subterminal	dorsally		
71	Oral disc orientation	ventrally	antéroventrally	anteriorly	anterodorsaly	dorsally	
72	Oral disk visibility dorsally	not visible	visible				
73	Papillae	absent	present				
74	Papillae size	no papillae	small sized papillae	moderatelly sized papillae	big sized papillae		
75	Marginal papilae length	absent	< 0,10 mm (very short)	0,10 - 0,20 mm (short)	0,20 - 0,30 mm (moderately long)	> 0,30 - 0,40 mm (long)	> 0,40 mm (very long)
76	Submarginal papilae length	absent	< 0,10 mm (very short)	0,10 - 0,20 mm (short)	0,20 - 0,30 mm (moderately long)	> 0,30 - 0,40 mm (long)	> 0,40 mm (very long)
77	Papillae form	no papillae	suctorial type	conical	rounded	elongated	
78	Papillae tip	no papillae	normal (rounded)	rounded with protuberance	pointed	MP rounded and SMP pointed tip	
79	Number of marginal papillae row	no papillae	single	double	triple		
80	Marginal papillae gap	no papillae	dorsal and ventral gap	dorsal gap only	ventral gap only	complete (no gap)	
81	Number of marginal papillae	no papillae	< 50 (very few)	50 - 100 (few)	100 - 200 (moderatelly many)	200 - 300 (many)	> 300 (too many)
82	Number of sumarginal papillae	no papillae	< 50 (very few)	50 - 100 (few)	100 - 200 (moderatelly many)	200 - 300 (many)	> 300 (too many)
83	Position of submarginal papillae on lower labium	no papillae	only ventrally	only lateraly	ventrolaterally	ventrolaterally + laterally	ventraly + ventrolateraly + laterally
84	Position of submarginal papillae on upper labium	no papillae	only dorsally	only lateraly	dorsolaterally	dorsolaterally + laterally	dorsaly + dorsolateraly + laterally
85	Papillae dorsal gap (DG) vs oral disk width (ODW)	absent	< 20% (very narrow)	20 - 40% (narrow)	40 - 60% (moderately wide)	60 - 80% (wide)	> 80% (very wide)
86	Papillae ventral gap (VG) vs oral disk width (ODW)	absent	< 20% (very narrow)	20 - 40% (narrow)	40 - 60% (moderately wide)	60 - 80% (wide)	> 80% (very wide)
87	Papillae visibility dorsally	no papillae	not visible	visible			
88	Keratodonts	absent	present				
89	Nb de rangées de kératodontes par bourrelet charnu labial	no keratodont	1	2			
90	Number of divided upper keratodont row	no keratodont or no divided upper row	1	2	3	4	> 5
91	First divided upper row	no keratodont or no divided upper row	A1	A2	A3	A4	> A5
92	Number of undivided upper keratodont row	no keratodont or no undivided upper row	1	2	3	4	> 5
93	Number of divided lower keratodont row	no keratodont	0	1	2	3	
94	First undivided lower row	no keratodont	no undivided lower row	P1	P2	P3	
95	Number of undivided lower keratodont row	no keratodont	0	1	2	3	
96	Keratodont length	no keratodont	< 0,05 mm (very short)	0,05 - 0,10 mm (short)	0,10 - 0,20 mm (moderately long)	0,20 - 0,30 mm (long)	> 30 mm (very long)

97	A1 length: A1 vs ODW	no keratodont	< 20% (very short)	20 - 40% (short)	40 - 60% (moderately long)	60 - 80% (long)	> 80% (very long)
98	Distal keratodont size	no keratodont	same length as those in the middle	medial lenghted	shorter		
99	Keratodont rows state	no keratodont	intact	scattered			
100	Keratodont rows alignement	no keratodont	regular	irregular			
101	Lower keratodont rows formed a chevron	no keratodont	no	yes			
102	(A2 gap) vs row length (A2)	no gap	< 20% (very narrow)	20 - 40% (narrow)	40 - 60% (moderately wide)	60 - 80% (wide)	> 80% (very wide)
103	P1	no keratodont	not interupted	interupted			
104	Space between marginal papilae and keratodont row	no keratodont or no papillae	tight	prominent			
105	Jaw sheath type	absent	reduced	generalized (typical with smooth surface)	ribbed (giving the appearance of vertical bars)	long spikelike derivative	Cowani like
106	Jaw sheaths state	absent or not applicable	souple	strong	very strong		
107	Jaw sheath serration	no jaw sheath or not applicable	smooth edge	rounded serrations	pointed serrations	finely pointed serrations	hypertrophied serrations
108	Jaw sheath width (JW) vs oral disk width (ODW)	no jaw sheath	< 20% (very narrow)	20 - 40% (narrow)	40 - 60% (moderately wide)	60 - 80% (wide)	> 80% (very wide)
109	Upper jaw sheath presence	always present	absent or vestigial	always absent or not aplicable	highly modified		
110	Upper jaw sheath medial convexity length (MCL vs JW)	no jaw sheath or abs or not aplicable	< 10 % (very short)	10 - 20 % (short)	20 - 30 % (moderately long)	30- 40 % (long)	> 40 % (very long)
111	Upper jaw sheath medial convexity shape	absent	wide rounded	narrow rounded	wide pointed	narrow pointed	elongated
112	Upper jaw sheath coloration	no jaw sheath	not keratinized	partially keratinized	fully keratinized		
113	Lower jaw sheath coloration	no jaw sheath	not keratinized	partially keratinized	fully keratinized		
114	Lower jaw sheath shape	no jaw sheath	not applicable	U-shaped	V-shaped		
115	Lower jaw sheath visibility	no jaw sheath	not hidden by upper jaw sheath	partially hidden by the jaw sheath	totally hidden by upper jaw sheath		
116	Pigmentation pattern	uniformly paterned	spotted to blotched	reticulated			
117	Lateral space under the skin	absent	perceptible	obvious			
118	TMH/TH	< 20% (very low)	20 - 40% (less developed)	40 - 60% (moderately developped)	60 - 80% (developed)	> 80% (well developed)	
119	lower jaw sheath	abs	wider than higher	higher than wider			

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Mandria am-piadanana ry Neny Malala!

Lebenslauf

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